EXPLORING THE POTENTIAL ROLE OF LATE STAGE PREDATION AND CHINOOK SALMON AGE STRUCTURE

By

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Abstract

Chinook salmon (*Oncorhynchus tshawytscha*) populations across the North Pacific have displayed a decrease in body size-at-return resulting from declines both in age- and body size-at-maturity. These changes have precipitated the loss of the oldest age classes in some populations and have occurred throughout the range of this species, suggesting a shared – yet currently unknown – driver in the common marine environment. A hypothesis for the cause of these changes is intense and/or selective predation marine mortality after the first winter in the ocean, potentially from predators selectively removing relatively large sub-adult Chinook salmon. Here I consider the question: *under what circumstances could predation on large sub-adult individuals by salmon sharks (Lamna ditropis) change the age structure of a Chinook salmon population*? To address this question, I first estimated total per capita prey consumption by salmon sharks – an increasingly acknowledged predator of salmon on the high seas – using three methods: 1) daily ration requirement, 2) bioenergetic mass balance, 3) and a von Bertalanffy growth model. Second, I examined the effects of additional predation on an indicator Chinook salmon population from the Yukon River by simulating alternative predation scenarios with a stage-structured life cycle model. Scenarios described the strength and selectivity of predation, and the resulting simulated age structure was then compared to observed demography. The selectivity and intensity of removals required to produce this change in age structure were considered in the context of top predators, focusing on salmon sharks. The daily ration method yielded individual salmon shark consumption estimates of 1461 and 2202 kg·yr-1, the mass-balance method produced estimates of 1870 kg·yr-1, 2070 kg·yr-1, 1610 kg·yr-1, and 1762 kg·yr-1, depending on assumed diet, and the growth model output estimates of 16,900 kg·yr-1 or 20,800 kg·yr-1, depending on assumed assimilation efficiency. The per capita prey consumption estimates from the mass-balance method may be the most realistic because they incorporated life history data specific to salmon sharks and did not produce extreme values. Taken as a whole, these estimates suggest salmon sharks have energetic requirements similar to those of

piscivourous marine mammals and corroborates conclusions of previous research suggesting that endothermic fishes exhibit metabolic rates similar to marine mammals. The simulated mortality scenarios that most closely mimicked observed shifts in age structure of the indicator Chinook salmon population focused intense and selective predation on the third year of Chinook salmon residence in the ocean. This simulated predation is corroborated by emerging results from an independent electronic tagging study in which tagged Chinook salmon experienced high predation rates, and research suggesting that killer whales (*Orcinus orca*) selectively prey upon Chinook salmon in their third year at sea. In summary, salmon sharks likely have high energetic requirements that could result in a large biomass of prey consumed, Chinook salmon populations are sensitive to predation during the third ocean year, and salmon sharks and other predators appear to frequently consume fish at that ocean stage. Taken together, these lines of evidence point to a potentially important mechanism for top down pressure on Chinook salmon populations that may explain observed changes in age-at-return, which in turn can affect population productivity. Future work and more robust data on predator distributions and abundances are needed to explore this finding further.

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General Introduction

Changes in size and age at maturity have been well documented in fish populations experiencing top-down pressure from fisheries or other natural predators. The ecological consequences of these demographic changes, such as reduced fecundity or offspring quality, have been hypothesized to reduce productivity of populations (Healey 1991; Marteinsdottir and Thorarinsson 1998), such as for Atlantic cod (*Gadus morhua*) (Olsen *et al.* 2004) and North Sea plaice (*Pleuronectes platessa*) (van Walraven *et al.* 2010). Reduced productivity can result in less surplus production available for harvest, and is especially of concern for imperiled species that are failing to recover despite reduction in fishing mortality or fishery closure (Murawski *et al.* 2001; Enberg *et al.* 2009). Similar changes in age and size at maturity have been demonstrated in controlled predation experiments. For example, guppies (*Poecilia reticulata*) exposed to high predation environments were observed to mature earlier and at smaller sizes (Reznick and Ghalambor 2005) than those in low predation environments, even when moved into a common garden experiment, consistent with contemporary evolutionary change. Recognizing populations with truncated age structures and identifying the cause of these demographic changes is a step toward understanding why imperiled stocks have failed to recover and development of better informed management for stock rebuilding.

Pacific salmon (*Oncorhynchus* spp.) have decreased in size at return to their natal rivers throughout the Pacific basin, though the magnitude of the trend varies regionally and among species. This trend was reported several decades ago (i.e. Ricker 1981; Bigler *et al.* 1996) and more evidence has amassed over time. Despite the size-dependent nature of maturation in *Oncorhynchus* spp. (Hankin *et al.* 1993; Morita *et al.* 2005), populations of Chinook salmon (*O. tshawytscha*) have also shown a paradoxical decline in age at maturity in conjunction with a decreased size at maturity (Lewis *et al.* 2015; Ohlberger *et al.* 2018), when an increase in age at maturity would have been expected given relationships

between growth and maturation. The earlier age at maturity has resulted in a loss of the oldest age classes in many Chinook salmon populations. The most pronounced shifts in age structure of Chinook salmon have occurred in Alaska, the northern-most part of their range (Ohlberger *et al.* 2018). In these populations, the proportion of age ocean-age 4 (1.4, or total age 6) has declined from being the dominant age class in spawning areas and ocean-age 2 and 3(1.2 and 1.3, age 4 and 5) fish have become the dominant age classes on the spawning grounds in recent years. Additionally, the oldest, largest fish, ocean-age 5 and older (1.5, age 7), have become exceedingly rare and have disappeared altogether from many spawning areas (Lewis *et al.* 2015). This change in age structure is particularly concerning because the abundance of Chinook salmon is also declining throughout its range and the ecological consequences of losing the oldest and largest spawners could inhibit the recovery of this culturally iconic species.

Chinook salmon are the largest bodied and most highly valued species of Pacific salmon, though among the least numerically abundant. They are caught in recreational, commercial, and subsistence fisheries and their native range along North America spans from Kotzebue Sound, Alaska to the Sacramento-San Joaquin River system, California (Healey 1991, Kreuger *et al.* 2009). *O. tshawytscha* is a semelparous species, dying after spawning, and anadromous, reproducing in their natal freshwater habitat after obtaining the vast majority of their growth at sea. Populations where some of the most drastic size and age structure changes have been observed are at the northern extent of the species' range, including the Yukon and Kuskokwim rivers in western Alaska. Fish from these populations largely display stream-type life histories (Royer *et al.* 2004), where they migrate to the ocean after a year in freshwater and return to their natal river months in advance of spawning (Healey 1991). Once in the marine environment, these populations remain in nearshore waters through their first ocean summer and fall (Royer *et al.* 2004). During their residence in the ocean, they travel extensively within the Bering Sea (Larson *et al.* 2013) and generally comprise at least 50% of the mixed Chinook salmon stock in the eastern Bering

Sea/Aleutian Island Region, as evidenced from bycatch in offshore fisheries (Myers *et al.* 1987; Myers and Rogers 1988; Larson *et al.* 2013).

Though the causes of the changes in size and age of Chinook salmon remain unclear, the wide geographic extent of the phenomenon suggests that all populations have been exposed to a shared common driver to varying degrees that likely occurs during the marine phase. The disappearance of older age classes in conjunction with fish returning at smaller sizes indicates intense and/or selective predation may occur after the critical periods of ocean entry and the first ocean winter (Beamish and Mahnken 2001; Beamish *et al.* 2001; Schindler *et al.* 2013; Ruggerone 2016). Over time, a more dangerous ocean could preferentially select for early maturity in Chinook salmon, while the fish are still small, through the reduced probability of older fish returning to spawn. This scenario could eventually result in a genetic change in the maturation schedule of these populations. This phenomenon has been observed in brook trout (*Salvelinus fontinalis*) in high mortality environments where earlier age at maturation overrode the fitness benefits associated with longer growth periods, resulting in younger spawners (Hutchings 1996).

Generally, the specific mechanisms of mortality during the oceanic life stage of salmon species, especially after their first year at sea, are poorly understood (Ruggerone and Nielsen 2009; Drenner *et al.* 2012)[1]. Some potential causes of marine mortality include: bycatch in marine fisheries, size selective harvest, and changes in the predatory gauntlet of the marine environment. Large-scale climatic phenomena that drive environmental conditions in the North Pacific Ocean, such as the Pacific Decadal Oscillation (PDO), have previously been linked to salmon survival and productivity (Mantua *et al.* 1997; Hare *et al.* 1999; Ohlberger *et al.* 2016). However, recent work suggests that the PDO has not been well correlated with salmon abundance in recent decades (Litzow *et al.* 2014; Litzow *et al.* 2016). Upon

[1] In a synthesis of literature on the marine life of salmonids Drenner *et al.* (2012) found a "definite lack of research on salmonid survival and mortality at sea." Ruggerone and Nielsen (2009) went so far as to say, "…scientists do not know how salmon die at sea… little quantitative information on predators of salmon at sea is available."

investigating the impacts of bycatch on western Alaskan Chinook salmon, Ianelli and Stram (2014) showed that bycatch in the largest fishery in the North Pacific Ocean is not thought to contribute to the observed changes in Chinook salmon populations. While size selective harvest has almost certainly played a role in the changes (Bromaghin *et al.* 2008), Ohlberger *et al.* (2018) discussed several potential causes including harvest and concluded that exploitation rates in coastal fisheries has declined as demographic changes have accelerated, indicating that size selective harvest is likely not the only cause. Additionally, Kendall and Quinn (2011) concluded that opposing selection by different fishing sectors suggested other factors likely contributed to observed size and age trends. Changes in the predator field faced by Chinook salmon in the ocean is the least examined cause of selective mortality, though evidence of top down effects by predators on Chinook salmon has been increasing. Marine mammals have been shown to consume a significant amount of Chinook salmon (Williams *et al.* 2004; Ford and Ellis 2006; Adams *et al.* 2016; Chasco *et al.* 2017). Additionally, emerging electronic tagging research on Chinook salmon provides evidence of frequent predation events in Alaskan waters. A unique temperature signature collected by the tag after inferred ingestion of an externally tagged Chinook salmon suggests that the vast majority of these predation events were attributed to salmon sharks (*Lamna ditropis*) (Goldman *et al.* 2004; Seitz *et al.* 2016). This pattern was common, seen in 14 out of 35 recovered tag time series, and was widespread in the Bering Sea/Aleutian Island region (Seitz and Courtney 2016). The identification of a single predator species frequently consuming Chinook salmon after their first ocean winter provides a basis for evaluating the consumption and selection potential for this predator.

In the North Pacific, salmon sharks are large opportunistic predators (Hulbert *et al.* 2005; Williams *et al.* 2010; Bizzarro *et al.* 2017). Adult salmon sharks range from 180 to 210 cm pre-caudal length (PCL), can weigh more than 220 kg, and can live to over 30 years in age (Nagasawa 2002; Goldman and Musick 2006). This species is widely distributed in the region (35°N–70°N) (Compagno 1984; Mecklenburg *et al.* 2011) and both ontogenic and sexual spatial stratification has been observed in

the population. Most sharks observed at the northern extent of this species' range are sexually mature (Goldman and Musick 2008; Carlisle *et al.* 2011), while parturition of live young, known as pups, is thought to occur at the southern end of the range (Weng *et al.* 2005; Goldman and Musick 2006; Carlisle *et al.* 2014). Juvenile sharks of an intermediate age have been observed stranded along the west coast of the United States (Carlisle *et al.* 2015). Additionally, the western North Pacific appears to be dominated by males, while the eastern North Pacific appears to be dominated by females (Hulbert *et al.* 2005; Gallucci *et al.* 2008). As with all lamnid sharks, salmon sharks are endothermic and maintain a body temperature differential of 18–21°C above ambient (Goldman *et al.* 2004), which is the highest of the lamnids. While endothermy is almost certainly adaptive by increasing the foraging success of salmon sharks in cold and highly productive northern waters, it likely comes at a high energetic cost (Block and Finnerty 1994; McNab 2002; Watanabe *et al.* 2015a). The overall abundance and distribution of salmon sharks in the region is unknown.

The consumption of Chinook salmon by *L. ditropis* in both summer and winter and over a large geographic area suggests that this mechanism of mortality could be more significant than was previously considered. Though salmon sharks appear to generalist predators, their consumption of Chinook salmon could be size selective due to the higher food gain to handling time ratio of consuming larger prey (Pyke 1984). Thus, removal of large Chinook salmon by these sharks could act as a selective pressure and contribute to the observed decline in size-at-age/age-at-return. Additionally, Hulbert and Rice (2002) calculated a coarse consumption estimate for salmon sharks around Port Gravina, Prince William Sound and concluded that, "low [pink] salmon runs at times of high salmon shark survival could be devastating until shark numbers decline or redistribute (switch prey) away from adult salmon staging areas." Given the sustained depression of Chinook salmon stocks and unexplained changes in size-at-age and age-at-maturity of this species, it is pertinent to examine unstudied sources of marine mortality, such as salmon sharks. Here, I took the first steps toward estimating the potential levels of Chinook salmon consumption

by salmon sharks using a range of available information and methods. Additionally, I investigated the potential contribution of predators to a "dangerous ocean hypothesis" by performing simulations with a modified version of a published Chinook salmon population dynamics model that already has included environmental covariates and bycatch, but not marine mortality after the first ocean winter.

Study Objectives

This goal of this study is to elucidate how much and how selective additional predation would be need to be in order to explain the observed age structure changes in Chinook salmon populations and to consider that level of predation mortality in light of potential consumption by salmon sharks. I hypothesize that age structure changes observed in Chinook salmon populations are driven by selective mortality after the first ocean winter and that salmon sharks may impose at least some of that mortality. This hypothesis will be investigated using the following objectives:

1. Estimate a range of potential per capita annual consumption levels for adult salmon sharks.
2. Examine the response of an indicator Chinook salmon population to predation by investigating the sensitivity of the Chinook salmon to predation on different ocean age classes.

I addressed the first objective by performing a meta-analysis using available information from salmon sharks, other sharks, and other endothermic fishes, and using multiple methods to produce estimates of yearly prey consumption per individual, adult salmon shark. I employed a multimodel comparison approach to address the scarcity of information on the species of interest by leveraging disparate data sources to generate multiple predictions for the same quantity of interest. Borrowing parameter values from other life stages and species is a widespread issue in the area of bioenergetics and consumption estimation (Trudel *et al.* 2004). However, within fisheries science, a lack of support for basic research to estimate the parameters required in bioenergetics models has been noted (Ney 1993), making the practice difficult to prevent. We acknowledge that borrowing values may be problematic and

in an effort to avoid "unjustified species borrowing" (Ney 1993), we prioritize values from species within the lamnid family, whenever possible. Generating three independent estimates for annual per capita consumption allows the difference between results to act as a measure of uncertainty; if all methods produce similar results it is a qualitative indication of accuracy. The three methods we used to calculate per capita consumption rates were: 1) daily ration requirement, 2) bioenergetic mass balance, 3) and a Bayesian model of shark growth. These models were selected because they have different levels of complexity, data requirements, and limitations. The first method was chosen because it is not data intensive; the second is a method used for other endothermic fishes (Schindler *et al.* 2002; Wood *et al.* 2009), but with known weaknesses due to the practice of parameter-borrowing; and the third tries to reduce the data needs of estimating consumption by using size-at-age data, but has received less study and validation. Using three methods provides a better estimate of uncertainty than any method in isolation since we do not have field data against which to compare our results at this time.

A daily ration requirement is the average percent of an individual's body mass that is consumed daily (% body mass·day^{-1}); this method serves as a rough initial estimate of consumption. Bioenergetic mass balances estimate the sum of an animal's energy expenditures to calculate how much energy an animal must consume to meet those requirements. Bioenergetic methods allow the estimation of energetic requirements for organisms that are otherwise hard to sample, such as large-bodied, highly-migratory fishes like salmon sharks. However, these methods can be data intensive as they require values for a suite of life history parameters to be specified. The Bayesian model of shark growth attempts to alleviate some of the parameter requirements for calculating consumption by using length (or weight)-at-age data, which can be more readily available for these hard to study species. This method has been applied and verified in tunas (Essington *et al.* 2001), another large endothermic fish, but has not yet been applied to lamnid sharks. By applying three methods we can evaluate if methods corroborate one another and we can highlight key pieces of missing information for future research.

I addressed the second objective by investigating the potential contribution of predators to a "dangerous ocean hypothesis" by performing simulations with a modified version of a published Chinook salmon population dynamics model (Cunningham *et al.* 2018). The existing model contains environmental covariates and bycatch, but not additional late marine stage mortality after the first ocean winter. I extended the model to include additive mortality to the late marine stage to retrospectively elucidate how much and how selective additional predation must be to mimic the trends in age structure observed in an indicator Chinook salmon population.

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Chapter 1: Prey consumption estimates for salmon sharks[2]

Abstract

As a first step towards better understanding the average annual prey consumption for individual adult salmon sharks (*Lamna ditropis*), an apex endothermic predator of North Pacific Ocean, we bracket consumption estimates using three methods: 1) daily ration requirement, 2) bioenergetic mass balance, and 3) a Bayesian model of shark growth. In the first method, we applied ration estimates for related lamnid shark species that yielded salmon shark estimates of 1461 and 2202 kg·yr-1. The second method used a mass-balance technique to incorporate life history information from salmon sharks and physiological parameters from other species and produced estimates of 1870 kg·yr-1, 2070 kg·yr-1, 1610 kg·yr-1, and 1762 kg·yr-1, depending on assumed diet. Growth modeling used salmon shark growth histories and yielded estimates of 16,900 kg·yr-1 or 20,800 kg·yr-1, depending on assumed assimilation efficiency. Of the estimates, those from the mass-balance may be the most realistic because they incorporated salmon-shark life history data and do not produce extreme values. Taken as a whole, these estimates suggest salmon sharks have similar energetic requirements to piscivourous marine mammals and corroborates conclusions of prior work that endothermic fishes are similar to marine mammals in metabolic rate.

Introduction

Top predators can influence the abundance and population structure of lower trophic level organisms through direct effects, such as predation mortality, and indirect interactions, such as eliciting risk averse behaviors of prey that have fitness consequences (Estes 1998; Frank 2005; Ainley 2007). In marine ecosystems, including the North Pacific, large sharks such as the salmon shark (*Lamna ditropis*) are generally considered to be positioned at a high trophic level (Wetherbee *et al.* 2004;

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[2] Manishin, K.A., Goldman, K.J., Short, M., Cunningham, C.J., Westley, P.A.H., and A.C. Seitz. *In press.* Prey consumption estimates for salmon sharks. Marine and Freshwater Research.

Heithaus *et al.* 2010). Several studies have investigated the influence of top predators on the abundance of their prey despite the logistical challenges of studying large, highly mobile species (Estes 1998; Frank 2005; Ainley 2007; Navia *et al.* 2010; Bornatowski *et al.* 2014). For example, in the North Atlantic, in and outside the Bay of Fundy, high predation rates in the coastal zone by porbeagle sharks (*Lamna nasus*) and Atlantic bluefin tuna (*Thunnus thynnus*) may contribute to the poor recruitment of local Atlantic salmon (*Salmo salar*) (Lacroix 2014). Determining the influence of predators on their prey requires knowledge of diet, energetic requirements, and population size of the predator, as well as demographic information of prey populations (Williams *et al.* 2004).

Salmon sharks (*Lamna ditropis*, family Lamnidae) are widely distributed in the North Pacific region (35°N–70°N) (Compagno 1984; Mecklenburg *et al.* 2011). Females have a two year reproductive cycle and make parturition migrations to the southern end of their range where live young, known as pups, are born and move north with increasing size and age (Weng *et al.* 2005; Goldman and Musick 2006; Carlisle *et al.* 2014). Most individuals at the northern extent of this species' range are sexually mature, which occurs at ages 3 – 5 years and 125 – 145 cm precaudal length (PCL) for males and ages 6 – 9 and 160 – 180 cm PCL for females (Goldman and Musick 2008; Carlisle *et al.* 2011). Sexual segregation has been observed in the population; the western North Pacific appears to be dominated by males, while the eastern North Pacific appears to be dominated by females (Hulbert *et al.* 2005; Goldman and Musick 2008). As with all lamnid sharks, salmon sharks are endothermic and maintain a body temperature differential of 18–21°C above ambient (Goldman *et al.* 2004), which is the highest of the lamnids. While endothermy is almost certainly adaptive by increasing foraging success of salmon shark in cold, highly productive northern waters, it likely comes at a high energetic cost (Block and Finnerty 1994; McNab 2002; Watanabe *et al.* 2015a).

Salmon sharks are thought to be opportunistic generalists and have been observed to feed on Pacific salmon (*Oncorhynchus* spp.), squids, and other fishes including Pacific herring (*Clupea pallasii*)

and walleye pollock (*Gadus chalcogrammus*) (Hulbert *et al.* 2005; Williams *et al.* 2010; Bizzarro *et al.* 2017). Emerging electronic tagging research on large sub-adult Chinook salmon (*Oncorhynchus tshawytscha*) have shown evidence of frequent predation by salmon sharks in the Bering Sea/Aleutian Island region (Seitz and Courtney 2016). Chinook salmon is a culturally and ecologically important species currently expressing depressed population abundance and productivity through much of its range (Schindler *et al.* 2013; Ohlberger *et al.* 2016). The lack of recovery of Chinook salmon stocks, despite drastically reduced fishing pressure in some areas, has created great interest in identifying potential bottlenecks in population productivity (Brown *et al.* 2015; Ruggerone 2016). Though the causes of the population depression are unknown, the geographic extent of the phenomenon suggests that all populations have been exposed to its drivers to some degree, likely during their marine phase. The identification of a predator species frequently consuming Chinook salmon after their first ocean winter presents an opportunity to examine a potential mechanism of marine mortality for this salmon species. However, there is a paucity of information about salmon sharks from which to draw conclusions concerning this predator-prey relationship (Seitz *et al.* 2016). Three large missing pieces of information are yearly consumption per individual salmon shark, quantitative diet composition, and total population abundance.

Here we take the first steps toward estimating yearly prey consumption of individual, adult salmon sharks by gathering all available information on salmon sharks, other sharks, and other endothermic fishes, and using it in multiple consumption methods. We use a multimodel comparison approach to address the scarcity of information on the species of interest so that we may gather disparate data sources and generate multiple predictions for the same quantity of interest. Borrowing parameter values from other life stages and species is a widespread issue in the area of bioenergetics and consumption estimation (Trudel *et al.* 2004). However, within fisheries science, a lack of support for basic research to estimate the parameters required in bioenergetics models has been noted (Ney 1993),

making the practice difficult to avoid. We acknowledge that borrowing values may be problematic and in an effort to avoid "unjustified species borrowing" (Ney 1993), we prioritize values from species within the lamnid family, when possible. By generating three estimates we aim to triangulate an estimate of salmon shark consumption, in the same fashion one triangulates their position in navigation and the relationship between results can act as a measure of uncertainty.

The three methods we used to calculate per capita consumption rates were: 1) daily ration requirement, 2) bioenergetic mass balance, 3) and a Bayesian model of shark growth. These models were selected because they have different levels of complexity, data requirements, and limitations. A daily ration requirement is the average percent of an individual's body mass that is consumed daily (% body mass·day^{-1}), this method serves as simple, data light, starting point to get an idea of where consumption might be. Bioenergetic mass balances estimate the sum of an animal's energy expenditures to calculate how much energy that animal must consume to meet its energetic requirements. Bioenergetic methods allow the estimation of energetic requirements for organisms that are otherwise hard to sample, such as large-bodied, highly-migratory fishes, and has been used for other endothermic species (Schindler *et al.* 2002; Wood *et al.* 2009). However, these methods can be data intensive as they require data on a suite of life history parameters to be specified, which leads to known weaknesses due to the practice of parameter-borrowing. The Bayesian model of shark growth attempts to alleviate some of the parameter requirements for calculating consumption by using length (or weight)-at-age data, which can be more readily available for these hard to study species. This method has been applied and verified in tunas (Essington *et al.* 2001), another large endothermic fish, but has yet not been applied to lamnid sharks. Using three independent estimation methods for the same quantity allows comparison of alternative predictions. This type of multi-model inference is useful because we do not have field data against which to compare our results at this time and it allows us to highlight key pieces of missing information for future research.

Methods

Focus Region

Due to recent reports of predation by salmon sharks on prey species of cultural and ecological importance (Seitz *et al.* 2016) in the Bering Sea/Aleutian Islands region, this study focuses on that region, where adult salmon sharks are known to occur (Mecklenburg *et al.* 2011). Concentrating on this demographic and area was motivated by several observations of predation on Chinook salmon, combined with over a decade of low abundance of this species in the Bering Sea/Aleutian Island region (Gisclair 2009; Hilsinger *et al.* 2009; Howe and Martin 2009; Menard *et al.* 2009; Schindler *et al.* 2013; Poetter 2015).

Daily Ration Requirement

A daily ration requirement has not been calculated for this species. High and low estimates of daily ration for white sharks (Semmens *et al.* 2013) and shortfin mako sharks (Stillwell and Kohler 1982; Wood *et al.* 2009) (Table 1-1) were applied to the average mass of an adult salmon shark (132 kg, adapted from Goldman and Musick 2006) to get an approximation of biomass consumption in salmon shark-sized lamnids, as both white and shortfin mako sharks are larger bodies than salmon sharks. Because the values from related species do not contain a measure of uncertainty, the results are simple point estimates.

Bioenergetic Mass Balance

The bioenergetics approach for this study followed the form commonly used for teleost fishes, which has been applied to blue sharks (*Prionace glauca*) (Schindler *et al.* 2002) and shortfin mako sharks (Wood *et al.* 2009). The total annual energy required by an individual salmon shark (C_{nrg}), was calculated as the sum of energy used for metabolism, digestion (specific dynamic action), excretion (urine and feces), growth, and reproduction:

(1-1) $Cnrg = M + SDA + (F + Ur) + G + Rp$

where M = metabolism; SDA = specific dynamic action; F and Ur = excretion; G = somatic growth over one year; and Rp = reproduction. The estimate of annual energy required for an individual adult salmon shark was calculated by drawing 1,000 samples from the distribution of each model component where a standard deviation was reported (Table 1-2).

Metabolism (M) was assumed to be active metabolism since salmon sharks are obligate ram ventilators and must swim continuously to ventilate their gills. To estimate active metabolism, mean VO_2 was calculated using swimming speeds (U) from salmon sharks. Weng *et al.* (2008) reported median speed extrapolated from satellite tags and Watanabe *et al.* (2015) reported cruising speed from a speed sensor. An average of these speeds was taken and input into the following relationship from shortfin mako sharks, which was calculated as a least-squares regression between measured VO_2 and swimming speeds:

(1-2) $VO_2 = 506.42U + 201.39$ (Wood *et al.* 2009).

A sensitivity analysis was also conducted to examine the effect of using each swimming speed alone (Figure S1-1). VO_2 was then converted to energy consumed using the oxygen calorific constant of 13.6 $J \cdot mgO_2^{-1}$ (Schindler *et al.* 2002).

In the calculation of energy allocated to somatic growth (G), the parameters of a standard 3-parameter von Bertalanffy growth curve Equation 1-3 for salmon sharks reported by Goldman and Musick (2006) were used. For each replicate of estimation of consumption, a value was drawn from the range of values reported by Goldman and Musick (2006) for each growth function parameter (L_∞, maximum length; k growth rate; and t_o theoretical age at length zero) and the length at adult salmon shark ages (5 – 30 years) was calculated (Table 1-2).

(1-3) $Lt = L_\infty(1-exp(-K(t-t_o))$

Length-at-age was then translated to weight-at-age using the length-weight relationship reported by Goldman and Musick (2006). Growth per year for an adult salmon shark was estimated by subtracting weight the previous year (t-1) from weight at a given year (t). Average adult growth (in kilograms) for each replicate was calculated by taking the mean of these changes in weight. Finally, kilograms of growth were translated into megajoules (MJ) using the wet-weight energy density value of 5562 $kJ \cdot kg^{-1}$ from shortfin mako sharks (Wood *et al.* 2009), which was calculated from dry weight energy density of 20.6 $kJ \cdot g^{-1}$ measured by bomb calorimetry (Steimle and Terranova 1985), by assuming a 73% water content (Wood *et al.* 2009).

Energy for reproduction (Rp) was calculated for females and was assumed to be negligible for males (Wood *et al.* 2009). All sharks were assumed to be mature due to the northern location of the study region. The sex ratio was assumed to be 1:1 as the Bering Sea/Aleutian Islands region is where the western and eastern portions of the Pacific basin meet, and it is unknown if the sexual segregation displayed at lower latitudes is maintained in this region. Biomass allocated to pup production for females was calculated by assuming the following reproductive characteristics: mean litter size = 3.88 (Conrath *et al.* 2014), mean size at birth = 625 mm PCL (Tanaka 1980 in Nagasawa 1998), and 2-year reproductive cycle (Conrath *et al.* 2014); and an energy density value of 5562 $kJ \cdot kg^{-1}$ for pups (Wood *et al.* 2009). A normal distribution for pup length was created from the range reported by Tanaka (1980) in Nagasawa (1998), and a normal distribution of number of pups was specified by the mean and standard deviation reported by Conrath *et al.* (2014). Pup length and number of pups per litter were randomly drawn for each replicate. Pup length was then translated into weight following:

(1-4) $Weight = a \bullet Length^b$ (Goldman and Musick 2006), where a = 4.4E-0.5, and b = 2.875.

Total energy toward reproduction was calculated by multiplying pup weight and the number of pups in a litter. Energy towards reproduction was then discounted by the assumed sex ratio and biennial reproductive cycle. Finally, the estimated annual pup production in kilograms was translated into megajoules, using an energy density value of 5562 $kJ \cdot kg^{-1}$ for pups (Wood *et al.* 2009).

Energy used for digestion (*SDA*) and energy lost as waste (feces and urine, *F+Ur*) were a fraction of consumption. *SDA* was 10% of consumption estimated from small-spotted cat shark (*Scyliorhinus canicula*) using respirometry (Sims and Davies 1994 in Schindler *et al.* 2002), and excretion was 27% of consumption estimated from a juvenile lemon shark (*Negaprion brevirostris*) during a captive feeding study (Cortes and Gruber 1994 in Schindler *et al.* 2002). These values were used as they are from other elasmobranchs and were used by Wood *et al.* (2009) when calculating a daily ration requirement for shortfin mako sharks.

One thousand random samples were drawn from distributions specified for each term (Table 1-2) and summed to produce estimates of energy required per year by an individual shark ($kJ \cdot yr^{-1} \cdot individual^{-1}$). The final estimate of energy required by a salmon shark was calculated as the mean of these thousand iterations and the 95% interval around the estimate is the 2.5 and 97.5 percentile samples.

The output of bioenergetic mass balance was in terms of energy consumed and was translated into biomass using energy density values for common prey items (Table 1-3) (Nagasawa 1998; Hulbert and Rice 2002; Hulbert *et al.* 2005; Kubodera *et al.* 2007) and four hypothetical diet proportion scenarios, which divide prey between salmon, other fishes, and squid (Table 1-4). Salmon were divided by the five species of Pacific salmon (*Oncorhynchus* spp.) present in the study region extrapolating from Nagasawa (1998): 44% sockeye salmon (*O. nerka*), 31% chum salmon (*O. keta*), 17% pink salmon (*O. gorbuscha*), 13% coho salmon (*O. kisutch*), and 5% Chinook salmon. 'Other fishes' was divided arbitrarily and equally between herring, pollock, and sablefish (*Anoplopoma fimbria*). This conversion was made to facilitate comparison with the other methods. However, the scenarios are based on few data from a small

number of studies, requiring extrapolation of diet proportions. As such, these scenarios should be viewed as a necessary assumption to facilitate comparison in this study and not a representation of true quantitative proportions of prey in salmon shark diets. Due to the motivating observations of predation on Chinook salmon for this study, diet scenarios were designed to examine different levels of consumption of prey species of interest, namely Pacific salmon. Scenarios were designed based on the limited data that is available on salmon shark diets, and were intended to represent the shark diet during the summer ('high' salmon content), fall ('low medium' salmon content), and winter/spring ('low' salmon content) (Nagasawa 1998; Hulbert *et al.* 2005; Carlisle *et al.* 2011). For completeness, we added the 'high medium' scenario, which is not based on a season, but allows us to test a suite of diets that contain low, intermediate, and high salmon, other fish, and squid proportions. Though the diet scenarios were designed based on seasons, because of their extrapolative nature, we integrated each diet scenario over an entire year. Applying each scenario over an entire year instead of rotating seasonally allowed us to bracket any extreme values caused by low or high salmon consumption.

Bayesian Model of Shark Growth

The final method relies on the bioenergetic underpinnings of the von Bertalanffy growth function. This method was assessed by Essington *et al.* (2001) for endothermic Atlantic bluefin tuna (*Thunnus thynnus thynnus*) and was shown to work well. The growth function was fit in a hierarchical Bayesian framework, and parameter estimates were used to calculate annual consumption requirements. A hierarchical structure allowed growth parameters to be estimated for each individual, thus obtaining individual growth curves and taking the mean of those curves to approximate average growth in the population. This structure essentially treated the individual fish as a random effect, which prevented pseudo-replication that would have violated the independent and identically distributed assumption of the likelihood distributions (Zhang *et al.* 2009; Alós *et al.* 2010). In more general terms, individual growth parameters were assumed to arise from an overall distribution describing variation in the growth process

across individuals within the population. Using Bayesian estimation methods provided uncertainty in parameter estimates to be directly estimated (Gelman *et al.* 2014) and permitted the incorporation of prior information on salmon shark growth. The combined hierarchical Bayesian approach accounted for both individual and population variation.

We fit a generalized von Bertalanffy growth function (Equation 1-5) to length-at-age data, which was back-calculated from vertebral samples by Goldman and Musick (182 individuals, 2006).

(1-5) $L_t = L_\infty(1-\exp(-K(1-m)(t-to)))^{1/(1-m)}$,

where $m = db+1-b$, $E = (H/b)a^{(d-1)}$, $K = k/b$, and $L_\infty = (E/K)^{1/(1-m)}$.

Parameter L_t is length-at-age t, L_∞ is theoretical maximum length , k is energy loss constant, d is allometric slope of consumption, and H is the assimilation constant (eqn. 5, Essington *et al.* 2001). E and m are unit-less values introduced for mathematical convenience (Essington *et al.* 2001). This generalized form provides an unbiased estimate of consumption, in part, as it allows the allometric slope of consumption (d) to vary between individuals and the slope of length-weight regression (b) to be species-specific. The intercept (a, multiplier of length) and slope (b, the exponent on length) of length–weight regression, Equation 1-4, were estimated by Goldman and Musick (2006). The stochastic structure of the model was given by a normal likelihood for the shark length-at-age (L_t) where the mean was length-at-age of an individual shark and all individuals shared a common standard deviation (σ). Various semi-informative prior distributions were given for L_∞, K, m, t_o, and σ (Table S1-1). Prior distributions were specified based on previous fits of the von Bertalanffy growth function fit for salmon sharks (3-parameter, Goldman and Musick 2006) and endothermic tunas (*Thunnus* spp.) (generalized, Essington *et al.* 2001). The priors were constrained $0 < d < 1$ (Essington *et al.* 2001), and $t_o < 0$. The mechanistic part of the model resulted in all calculated shark lengths being positive, so it was not necessary to further constrain the values of shark length during the stochastic part of the model. Hyperpriors, the prior

distribution of a parameter of a prior distribution for a model parameter, were also designed to include previous estimates of model parameters. To aid convergence, all sharks shared a common shift parameter t_o instead of estimating a value of t_o for each individual shark (Alós *et al.* 2010). Other model values (*d, k, E,* and *H*) were calculated from the posterior means of the fitted parameters.

Markov Chain Monte Carlo simulations were used to generate samples from the posterior distribution for von Bertalanffy growth function parameters. Hamiltonian Monte Carlo was used in program Stan to efficiently sample all parameters from the posterior distribution simultaneously (Carpenter *et al.* 2017; Stan Development Team 2017; Monnahan *et al.* 2017). The growth model was fit by running the model three times (chains) from varied initial values for 100,000 iterations each. There was a 50,000 iteration burn-in/warm-up period to allow the algorithm to converge to the posterior distribution; the parameter values drawn during this period were discarded. Thinning was performed such that every 25th iteration was recorded. This resulted in a total of 4000 samples of each parameter for each shark from the posterior distribution. Traceplots and histograms of the parameter values drawn from the posterior distribution were used as a proxy of model convergence (Figure S1-2). Population level parameters were summarized as the mean of all individual parameters for each sample from the posterior distribution. The posterior means and 95% credible intervals were calculated for each parameter, these population level parameters are thus means of means. Due to the hierarchical structure of the model, a growth function was generated for each shark in the data set and an approximation of the true population level von Bertalanffy growth function is given by the population level parameter estimates.

Annual biomass consumed by an individual shark ($C_{biomass}$) was calculated using the assimilation constant, H, allometric slope of consumption, d, and assimilation efficiency, A, in Equation 1-7 (Essington *et al.* 2001; Pilling *et al.* 2002; Helser and Lai 2004). H and d were both calculated from the posterior means of the fitted von Bertalanffy parameters. The calculation of consumption was carried out twice, with two different values of assimilation efficiency. $A = 0.65$ was borrowed from tunas (family

Scombridae, Kitchell *et al.* 1978), which are endothermic fishes that are thought to have similar energetic requirements to salmon sharks (Watanabe *et al.* 2015a), and $A = 0.80$ for lemon sharks (*Negaprion brevirostris*), which is the only direct measurement of assimilation efficiency for a shark (Wetherbee and Gruber 1993). Assimilation efficiency was assumed to be constant across all body sizes (Essington *et al.* 2001).

(1-6) $C_{biomass} = (H/A)W^{d}W$

Results

The range of mean per capita consumption from all three methods was 577 – 20,800 kg·yr^{-1}.

Daily Ration Requirement

The potential consumption for lamnid sharks of salmon shark size estimated using the low and high daily rations from a white shark were 577 and 721 kg·yr^{-1}, respectively. The low and high daily rations a shortfin mako shark yielded annual prey consumption estimates of 1461 and 2202 kg·yr^{-1}, respectively (Top Panel, Figure 1-1) for a salmon shark sized lamnid.

Bioenergetic Mass Balance

The bioenergetic mass balance resulted in a slightly higher estimate of mean per capita consumption than the daily ration requirement. The total energy required by an adult salmon shark was estimated to be 8580 MJ·yr^{-1} (4110 – 13,400 MJ·yr^{-1}). When only swimming speed from Weng *et al.* (2008) was used, the energy consumption estimate was 7590 MJ·yr^{-1} (4110 – 10,800 MJ·yr^{-1}) and when only swimming speed from Watanabe *et al.* (2015) was used, the energy consumption estimate was 11,500 MJ·yr^{-1} (11,500 – 11,600 MJ·yr^{-1}). The effects of different swimming speed values on the final consumption estimate are plotted in Supplemental Figure S1-1. Energy requirement toward metabolism was estimated to be 5340 MJ·yr^{-1} (2540 – 8340 MJ·yr^{-1}), 25.5 MJ·yr^{-1} (22.3 – 28.8 MJ·yr^{-1}) was allocated toward growth, 38.1 MJ·yr^{-1} (8.9 – 96.4 MJ·yr^{-1}) toward reproduction, 2320 MJ·yr^{-1} (1110 – 3610 MJ·yr^{-1})

toward excretion, and 858 MJ·yr^{-1} (411 – 1340 MJ·yr^{-1}) toward specific dynamic action. Applying the 'low', 'low medium', 'high medium', and 'high' salmon consumption scenarios to the energetic needs of salmon sharks resulted in per capita consumption estimates of 1870 kg·yr^{-1} (740 – 2880 kg·yr^{-1}), 2070 kg·yr^{-1} (830 – 3220 kg·yr^{-1}), 1610 kg·yr^{-1} (640 – 2500 kg·yr^{-1}), and 1762 kg·yr^{-1} (706 – 2740 kg·yr^{-1}) (Mid Panel, Figure 1-1), respectively.

Bayesian Model of Shark Growth

The growth model produced the highest estimate of median per capita consumption 16,900 kg·yr^{-1} (95% Bayesian credible interval: 16,100 – 17,900 kg·yr^{-1}) when using an assimilation efficiency of A = 0.65 and 20,800 kg·yr^{-1} (19,800 – 22,100 kg·yr^{-1}) when using an assimilation efficiency of A = 0.80 (Bottom Panel, Figure 1-1). The von Bertalanffy growth function parameter estimates were L_∞ = 201 cm (200 – 202 cm), K = 0.255 (0.240 – 0.271), m = 0.165 (0.134 – 0.197), t_o = -1.34 years (-1.43 – -1.26 yrs), σ = 2.40 cm (2.32– 2.50 cm). The fitted model parameters resulted in calculated values of d = 0.710 (0.700 – 0.721), k = 0.731 kg·kg^{-1}·yr^{-1} (0.689 – 0.779 kg·kg^{-1}·yr^{-1}), E = 21.4 (19.91 – 23.8), and H = 3.21 kg·kg^{-d}·yr^{-1} (3.18 – 3.24 kg·kg^{-d}·yr^{-1}) (Figure 1-2).

Discussion

The daily ration method applied the ration requirements from related species as a way to approximate potential consumption for lamnid sharks of salmon shark size. Due to the physiological differences between salmon sharks and closely related lamnid species, these approximations could be underestimates. Salmon sharks maintain the highest difference between core and ambient temperature within Lamnidae, with a 18 – 21°C temperature differential. Shortfin mako sharks and white sharks exhibit a maximum of 8.0°C and 14.3°C , respectively. Additionally, both shortfin mako sharks and white sharks are larger bodied than salmon sharks, so they have greater thermal inertia, making it easier to maintain their elevated body and lowering their mass specific metabolism. Given the high temperature gradient and smaller relative body size of salmon sharks, it follows that they may require more prey to

fuel their thermal physiology (McNab 2002). Additionally, white sharks may consume less food mass because they eat a high percentage of energetically dense marine mammal blubber.

Since the bioenergetics mass balance incorporates salmon shark specific life history information it may be more realistic than the daily ration method. However, as with the daily ration requirement, information borrowed from other species may still cause the estimate from this method to be biased low. Specifically, the relationship between swimming speed and VO_2 was constructed for relatively small makos and physiological relationships have been shown to not scale linearly with body size (McNab 2002), so this relationship may be inaccurate for larger sharks. Next, the calculation of energy devoted to reproduction could be an underestimate for several reasons. First, our calculation only directly incorporates the energy required to produce the biomass, which is the pup, and does not account for other physiological stress due to pregnancy nor the parturition migration. The percent of total energy required for digestion (SDA) was borrowed from a small ectothermic shark. A major benefit of an endothermic strategy is that increased visceral temperatures allow more efficient break down of food items (Carey and Stevens 1984; Stevens and McLeese 1984). Therefore energy devoted to SDA may be lower in endothermic species, and this part of the calculation could be an overestimation. Should the previously described values, relationships and assumptions be incorrect, it is likely that the energetic requirements calculated from the mass balance are underestimates due to the inclusion of data from other, sleeker species that maintain cooler body temperatures in warmer habitats and the exclusion of energy toward a long distance migration and other reproductive costs.

The Bayesian model of shark growth used most species-specific data and hypothetically should provide the most realistic estimate of consumption for an adult salmon shark. However, the annual consumption rates generated by this method would require an extremely high daily ration (> 35% of the shark mass). This approach relies on the bioenergetic underpinnings of the von Bertalanffy growth function. This method was assessed by Essington *et al.* (2001) who found that calculating consumption

from fitted generalized von Bertalanffy growth function parameters worked well for endothermic Atlantic bluefin tuna (*Thunnus thynnus thynnus*), which have a decelerating growth rate. Salmon sharks are also endothermic with a decelerating growth, so we believed that the method would work comparably well for this species. However, Essington *et al.* (2001) also found that the estimates of consumption were very sensitive to the allometric slope of consumption, *d*, which we calculated based on fitted parameters from the generalized von Bertalanffy function. Due to the sensitivity of the estimate of this parameter, an avenue of future work could be to re-parameterize the model to fit *d* directly. We investigated such a parameterization, however we had difficulty with convergence and properly constraining other biologically relevant parameters under this structure. In conclusion, while this method suggests salmon sharks may have a high consumption rate, more investigation into the application of this method to this species should be conducted before drawing more definitive conclusions. Though the specific values generated in this study are likely over estimates, the results may suggest that salmon sharks have a high consumption rate, but a great deal of uncertainty remains.

The three methods used as a first step to estimate the annual prey biomass required for an individual adult salmon shark yielded estimates that spanned three orders of magnitude. This is an indication that the data we have attempted to use to describe salmon shark consumption is not sufficient and more species- specific data is required. Additionally, the magnitude of the disparity between our third result and the other two calls into question the accuracy of that method. Finally, due to the already limited data we were not able to examine sex-specific differences in consumption. However, salmon sharks do exhibit sexual dimorphism as females mature later and grow larger than males. While it would have been interesting, we do not have sufficient data to investigate these differences, but they could lead to sex-specific consumption requirements that may lead to differing effects on the prey populations in the Eastern and Western North Pacific due to sexual segregation. In the absence of in-situ observation or experimentation, we compare the three methods using the data limitations and outputs of each analysis.

Despite the caveats of each method for generating consumption estimates, we feel that the estimates from the mass-balance method may be the most realistic since they incorporate salmon-shark life history data, but do not produce extremely high values like the growth model. The estimate from this method suggests salmon sharks may have similar energetic requirements to piscivourous marine mammals that also use vascular counter current heat exchange to maintain their core temperatures (Scholander and Schevill 1955; Goldman *et al.* 2004).The energetic requirement of a killer whale is roughly 84 $MJ \cdot kg^{-1}$ of body mass annually (Williams *et al.* 2004). When mass corrected to the size of an average adult salmon shark, this results in an annual consumption of roughly 11,000 $MJ \cdot yr^{-1}$. For comparison, the mass balance estimate of energy required by a salmon shark, before conversion to mass, was 8580 $MJ \cdot yr^{-1}$. These results corroborate the conclusion of Watanabe *et al.* (2015) that fishes with red muscle endothermy are similar to marine mammals and birds in many respects, including high metabolic rate.

An obvious extension of this work is obtaining estimates of abundance for this predator and quantitative diet information to examine implications for prey species of interest at the population level. For illustrative purposes, we explored the biomass removed by an adult salmon shark population of a prey species, which makes up 3% of the shark diet using the mass-balance estimates. We used the theoretical populations values of 3000, 30,000, and 300,000 sharks. These values were selected because a small fishery in Japan harvests 3000 – 5000 sharks annual (K. Goldman per. comm., Paust and Smith 1986; Simpfendorfer *et al.* 2005). Additionally, during some years when high seas drift gillnetting was practiced, between 100,000 and 150,000 salmon sharks were caught as bycatch (Robinson and Jamieson 1984; McKinnell and Waddell 1993; Blagoderov 1994; McKinnell and Seki 1998; Tanaka and Davis 2002). Because salmon sharks are believed to be generalists and the impact of this biomass removal is likely spread across many species, we will examine a hypothetical prey item that represents 3% of the shark diet. At the lowest theoretical level of abundance, 3000 salmon sharks may consume between 145

and 190 t of our hypothetical prey item depending on the diet scenario, 30,000 sharks may consume between 1450 and 1900 t, and 300,000 sharks may consume between 14,500 and 19,000 t of this hypothetical prey item annually. For comparison, in 2017 commercial fisheries in Alaska harvested 1200 t of Chinook salmon (Alaska Department of Fish and Game 2018). If this species was to constitute 3% of the salmon shark diet, an intermediate shark population could remove as much Chinook salmon as recent commercial fisheries.

The wide range of estimated consumption rates leave too much uncertainty about the annual prey requirements of salmon sharks to draw definitive conclusions about their effect on prey species of interest, such as Chinook salmon. This work does highlight some knowledge gaps, which if filled could substantially improve consumption estimates. Species specific bioenergetic parameters and rigorously collected quantitative diet information will be required to obtain robust estimates of prey consumption at the individual level. Moving beyond individual consumption, estimates of overall salmon shark abundance will all be required to assess total prey consumption at the population level. Along with fisheries, marine mammals, and ectothermic fishes, salmon sharks should be viewed as one part of cumulative mortality sources of fishes in the North Pacific. The effect of predation by salmon sharks on a specific prey species will depend on the abundance and dynamics of the prey and the compensatory or additive nature of the mortality due to salmon sharks. If interest lies in understanding mortality of fish in the ocean, future work should include assessing the role of salmon sharks as predators in the North Pacific by aligning demographic information for the sharks and prey species in space and time to examine predator-prey interactions, when such data are available.

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Tables and Figures

Table 1-1: Daily ration requirements (% body weight·day-1) for two lamnid sharks.

Lamnid species		Daily Ration	Source
Shortfin mako shark	*Isurus oxyrinchus*	3.1– 4.58 %	(Stillwell and Kohler 1982), (Wood *et al.* 2009)
White shark	*Carcharodon carcharias*	1.2 – 1.5%	(Semmens *et al.* 2013)

Table 1-2: Inputs to the bioenergetic mass balance and their measure of variability for adult salmon sharks in the Bering Sea/Aleutian Islands region.

Input	Value	Variation	Source
Metabolism			
Mean swim speed	$U_1 = 0.51$ body length·sec^{-1}	SD (0.51, 0.18)	(Watanabe *et al.* 2015b)
	$U_2 = 0.18$ body length·sec^{-1}		(Weng *et al.* 2008)
Growth			
von Bertalanffy parameters	$L_\infty = 204.5$ cm	SD = 20.4	(Goldman and Musick 2006)
	$k = 0.18$	SD = 0.01	(Goldman and Musick 2006)
	$t_o = -2.2$	SD = 0.02	(Goldman and Musick 2006)
Reproduction			
Mean pup length	L = 62.5 cm	SD = 12.5	(Tanaka 1980 from Nagasawa 1998)
Mean litter size	N = 3.88 pups	SD = 0.13	(Conrath *et al.* 2014)

Table 1-3: Energy densities of common prey species of salmon sharks. Prey species are reported by Nagasawa (1998), Hulbert *et al.* (2005) and Carlisle *et al.* (2011).

Prey Item		Energy Density ($kJ \cdot kg^{-1}$ wet mass)	Source
Pacific salmon	*Oncorhynchus* spp.		
sockeye	*O. nerka*	7511	(O'Neill *et al.* 2014)
pink	*O. gorbuscha*	4786	(O'Neill *et al.* 2014)
chum	*O. keta*	4296	(O'Neill *et al.* 2014)
coho	*O. kisutch*	5815	(O'Neill *et al.* 2014)
Chinook	*O.tshawytscha*	7218	(O'Neill *et al.* 2014)
Other fishes			
pollock	*Gadus chalcogrammus*	3240	(Appendix B, Anthony *et al.* 2000)
herring	*Clupea pallasii*	5840	(Appendix B, Anthony *et al.* 2000)
sablefish	*Anoplopoma fimbria*	2640	(Table 3, Van Pelt *et al.* 1997)
Squid (various)	Mean (n=5)		
		5520	(Table 2, Perez 1994)

Table 1-4: Proportion of prey items in three theoretical salmon shark diet scenarios.

	Diet Scenario			
Prey Item	High	High Medium	Low Medium	Low
Pacific salmon	0.6	0.3	0.1	0.05
Other fishes	0.3	0.6	0.6	0.35
Squids	0.1	0.1	0.3	0.60

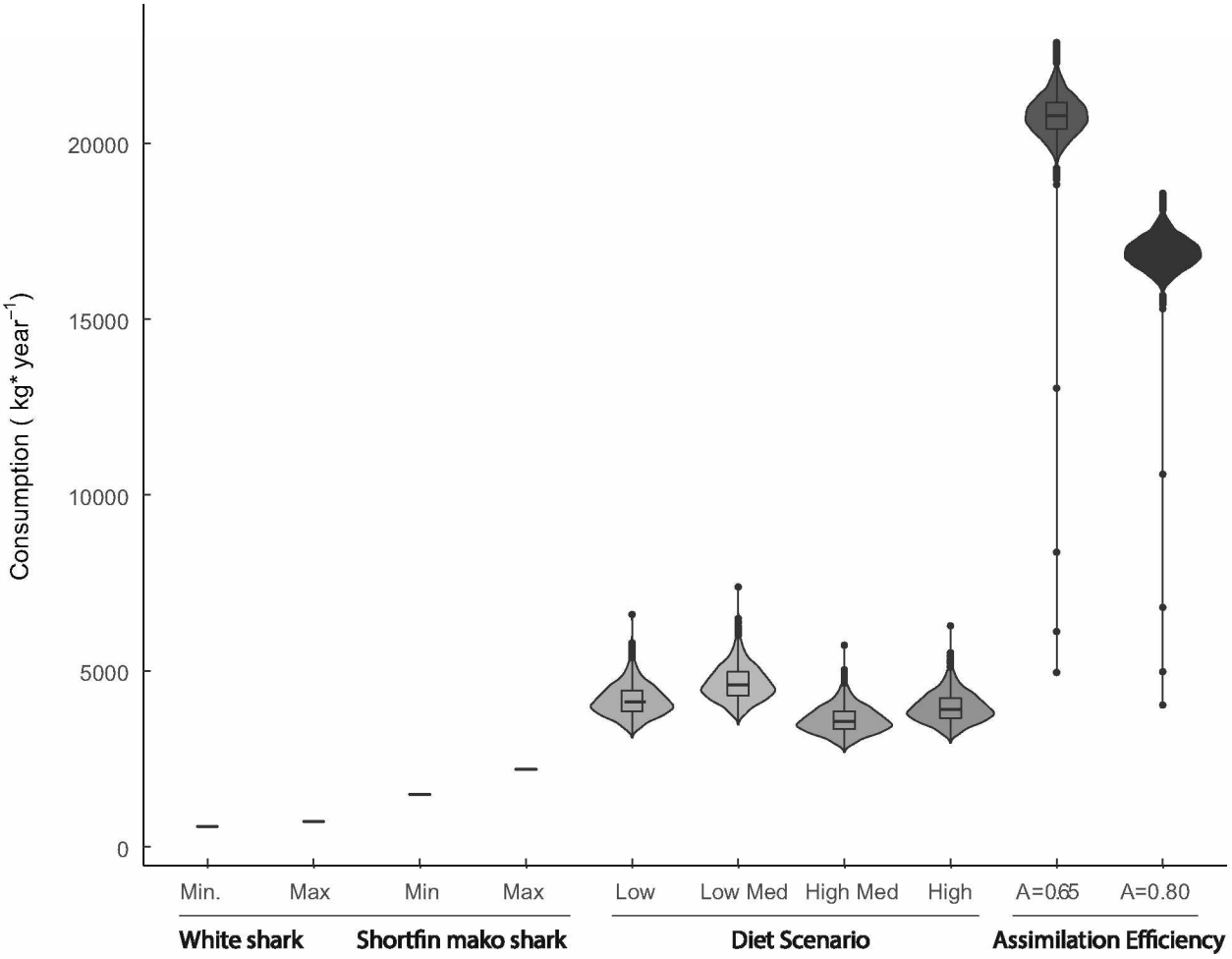

Figure 1-1: (Left) Prey consumption estimates in kilograms of prey consumed per year for individual adult salmon sharks based on the daily ration requirements for the closely related species white sharks and shortfin mako sharks, expressed as point estimates. (Middle) Prey consumption estimates for individual adult salmon sharks from the bioenergetic mass-balance in kilograms of prey consumed per year, visualized as violin plots containing box and whisker plots. From left to right are the 'low', 'low medium', 'high medium', and 'high' amount of Pacific salmon diet scenarios (Table 4). The bold center line of each box plot is the median while the lower and upper hinges are the 25th and 75th percentiles respectively. The whiskers extend 1.5 times the distance between the first and third quartiles, and any estimates beyond that range are plotted individually as points. The shaded area around each box and whisker plot is the violin area. The width of the violin plots is proportional to the probability density of alternative consumption rates. (Right) Prey consumption estimates of individual adult salmon sharks from the Bayesian model of shark growth in kilograms of prey consumed per year, visualized as above. From left to right are the estimates using the assimilation efficiency estimated for the Tuna family, another endothermic fish, and a lemon shark, another elasmobranch.

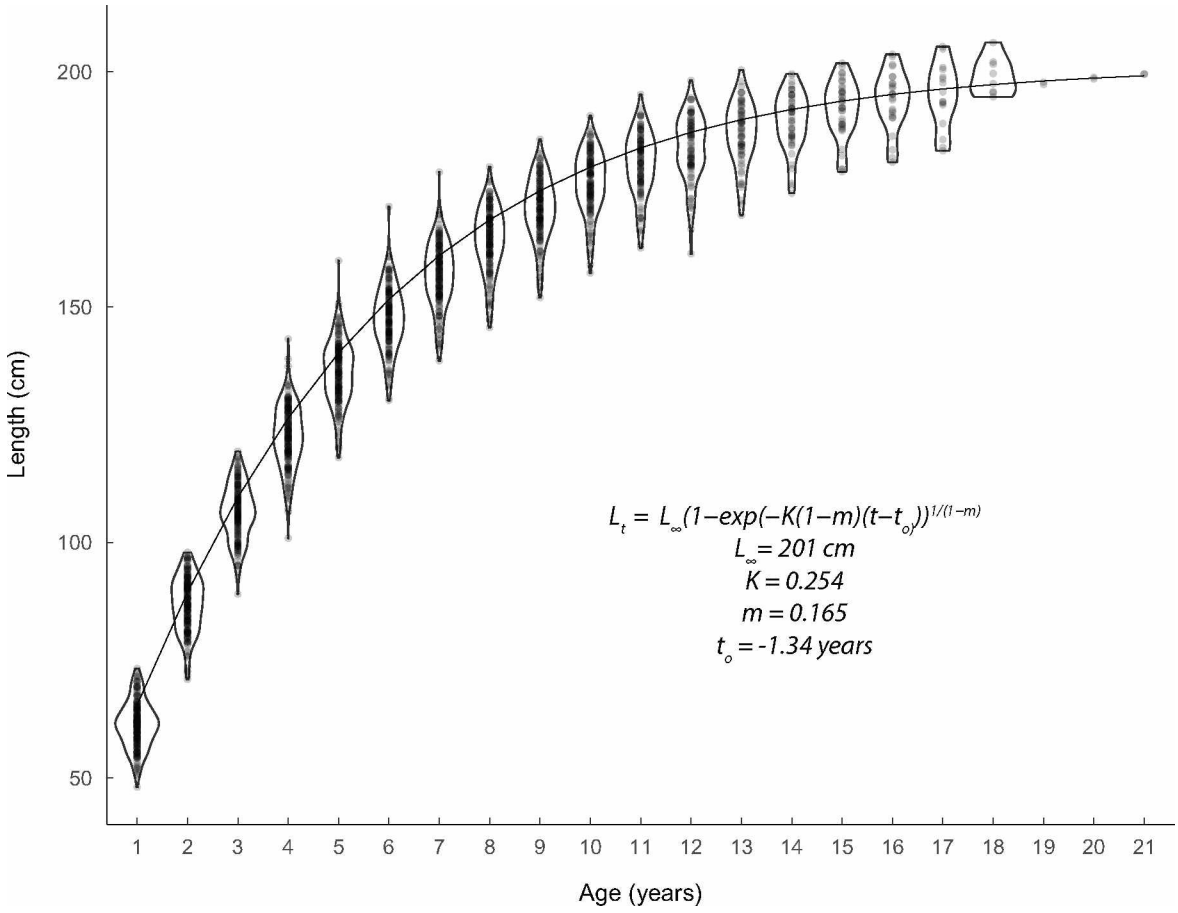

Figure 1-2: A generalized von Bertalanffy growth curve (solid line) of the form fitted to back-calculated length-at-age data (solid black circles) for salmon sharks. Around the back-calculated lengths are violin plots for each age. The height of the violin area is the total range of back-calculated lengths at that age and the width of the area is a mirrored distribution of the lengths at that age. Violin plots were not produced for the oldest ages, which contained few observations.

Supplementary

Table S1-1: Prior and hyperprior distributions of the von Bertalanffy growth function parameters L_∞, maximum length; K, energy loss or growth; m unit-less values introduced for mathematical convenience; t_o, theoretical age at which length is zero; and σ, the standard deviation of length-at-age for all individuals in the model. A hyperprior is a prior distribution on a parameter of a prior distribution.

Priors	Hyperpriors	
$L_\infty \sim \text{Normal}(\mu_{Linf}, \sigma^2_{Linf})$	$\mu_{Linf} \sim \text{Normal}(270, 10)$	$\sigma^2_{Linf} \sim \text{Normal}(15, 5)$
$K \sim \text{gamma}(\alpha, \beta)$	$\alpha \sim \text{Gamma}(2, 2)$	$\beta \sim \text{Gamma}(2, 2)$
$m \sim \text{beta}(\gamma, \delta)$	$\gamma \sim \text{Gamma}(7.5, 4)$	$\delta \sim \text{Gamma}(9, 4)$
$t_o \sim \text{normal}(-10, 5)$		
$\sigma \sim \text{uniform}(1E\text{-}3, 200)$		

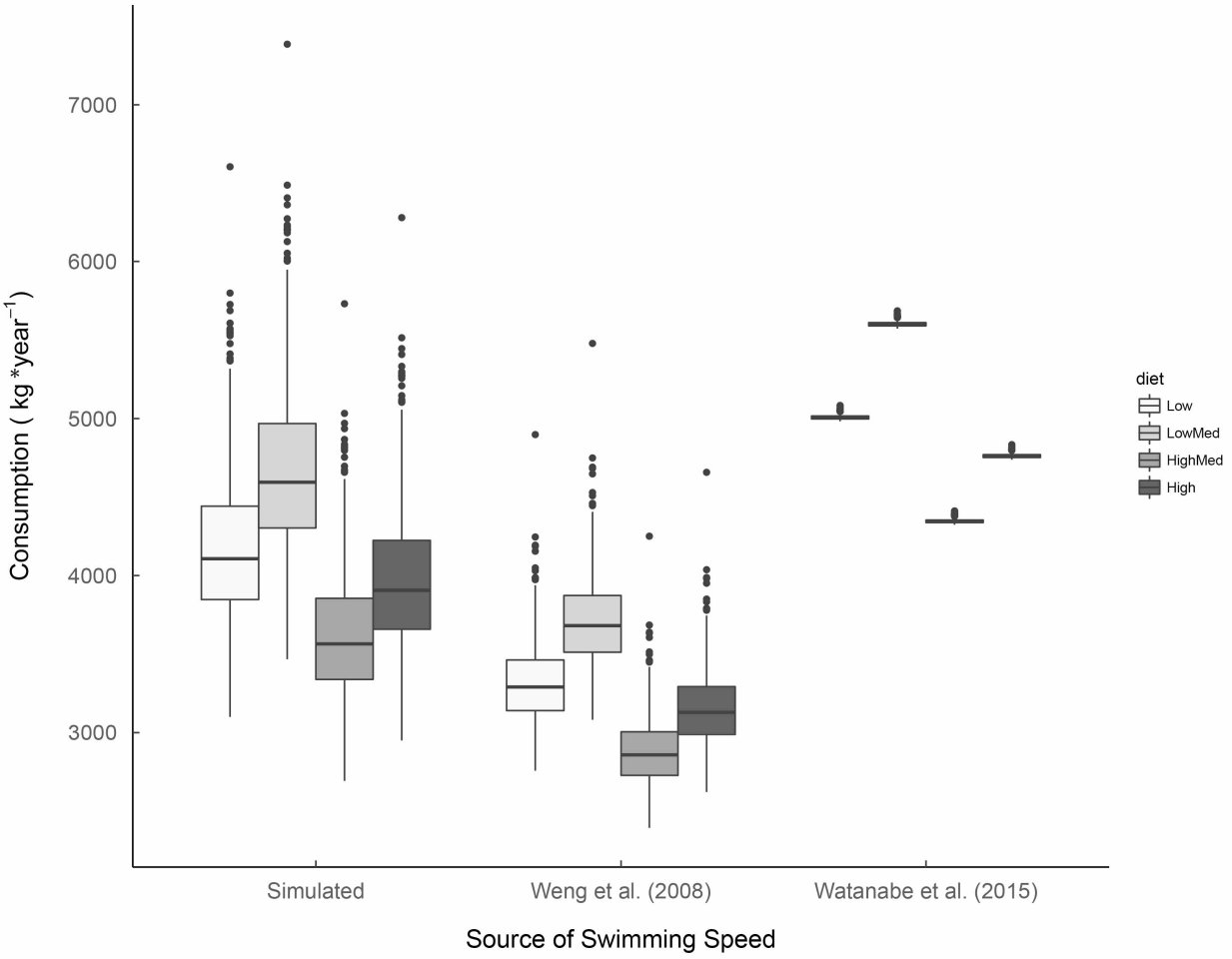

Figure S1-1: An examination of the sensitivity of per capita prey consumption estimates in kilograms of prey consumed per year to the specification of swimming speed during the mass balance model. From left to right are estimates using a swimming speed drawn from a normal distribution with the mean and standard deviation of the combined input speeds, next are estimates using only the speed range reported by Weng *et al.* (2008) and then the cruising speed measured by Watanabe *et al.* (2015). Estimates that included variability are represented as a box and whisker plot. The bold center line of each box plot is the median while the lower and upper hinges are the 25th and 75th percentiles respectively. The whiskers extend 1.5 times the distance between the first and third quartiles, and any estimates beyond that range are plotted individually as points.

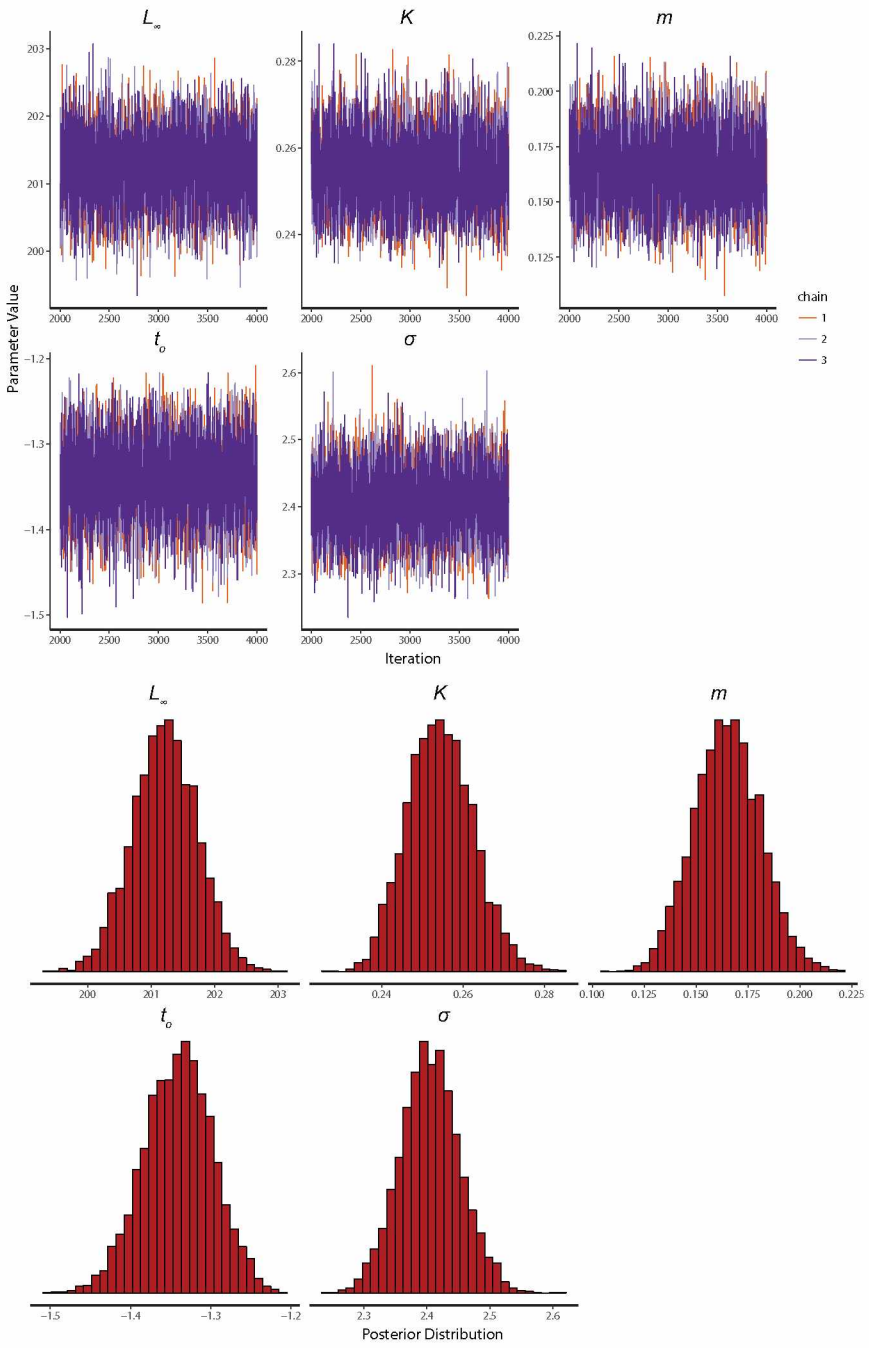

Figure S1-2: (Top Panel) Trace plots of von Bertalanffy growth curve parameters estimated for salmon sharks using a hierarchical Bayesian model. (Bottom Panel) Histograms of selections from the posterior distributions of von Bertalanffy growth curve parameters estimated for salmon sharks using a hierarchical Bayesian model. Together, the homogeneity of the trace plot and unimodal histograms were used as a proxy of convergence of the growth model.

Chapter 2 : Late stage marine mortality of Chinook salmon helps explain observed changes in age structure of a depressed Chinook salmon population

Abstract

Populations of Chinook salmon (*Oncorhynchus tshawytscha*) have declined in abundance throughout the Pacific Ocean basin while also returning younger and smaller at maturity than in the past. The most pronounced shift in age composition of spawning adults has occurred in Alaska, where the proportion of fish that spend four winters in the ocean has declined and those that have spent two and three winters at sea have become the dominant returning age classes. Parallel shifts in demography are occurring throughout the range of the species, suggesting that a shared perturbation in the common marine environment may be responsible. The traditional critical period/critical size hypotheses that focus on the first year in the ocean cannot explain the demographic changes, thus suggesting some period later in marine stage may play a role. Here we investigate whether selective mortality later in the marine stage could produce observed changes in age composition of a well-studied index population of Chinook salmon in the Yukon River watershed. To evaluate this question, we extended an existing stage-structured population dynamics model to include additional late marine mortality. The mortality scenarios that most closely re-created observed shifts in age structure of this population focused mortality during the third year at sea. This finding is supported by independent observations of wild predation events by killer whales (*Orcinus orca*) and salmon sharks (*Lamna ditropis*) on this ocean age class. These results demonstrate that marine mortality after that first year in the ocean may be responsible for the changes in age structure of adult spawners observed in many Chinook salmon populations. Taken as a whole, this compels a critical reexamination of the longstanding hypothesis that after the first few months at sea, the ocean is a fairly safe place for salmon.

Introduction

Changes in size and age at maturity have been well documented in fish populations experiencing top-down pressure from fisheries or other natural predators (Berkeley *et al.* 2004). The ecological consequences of these demographic changes, such as reduced egg/offspring quality, have been hypothesized to reduce productivity of populations (Healey 1991; Marteinsdottir and Thorarinsson 1998), such as for Atlantic cod (*Gadus morhua*) (Olsen *et al.* 2004) and North Sea plaice (*Pleuronectes platessa*) (van Walraven *et al.* 2010). Reduced productivity is of concern for imperiled species that are failing to recover despite reduction in fishing mortality or fishery closure (Murawski *et al.* 2001; Enberg *et al.* 2009). Evidence that changes in age and size at maturity are the result of adaptive contemporary life history evolution have been revealed from controlled predation experiments (Conover and Munch 2002; Reznick and Ghalambor 2005). For example, guppies (*Poecilia reticulata*) exposed to high predation environments were observed to mature earlier and at smaller sizes than those in low predation environments (Reznick and Ghalambor 2005), leading to the truncation of age structure in experimental populations. Recognizing populations with truncated age structures and identifying the causes of these demographic changes is a step toward understanding the lack of recovery by imperiled stocks and could lead to better informed management for stock rebuilding (Berkeley *et al.* 2004; Palkovacs 2011).

Chinook salmon (*Oncorhynchus tshawytscha*) have decreased abundance, age, and size-at-age at return to their natal rivers throughout the Pacific basin, though the magnitude of the trend varies regionally (Lewis *et al.* 2015; Ohlberger *et al.* 2018). The trends in size and age were reported several decades ago (i.e. Ricker 1981; Bigler *et al.* 1996) and more evidence has amassed over time. Like in other salmonids (e.g. Myers *et al.* 1986), sexual maturation in Chinook salmon is size dependent. Specifically, maturation has been linked to growth such that faster growing fish are expected to mature earlier than those under slower growth conditions (Clarke and Blackburn 1994; Wells *et al.* 2007). However, size-at-age of Chinook salmon has decreased (Lewis *et al.* 2015; Ohlberger *et al.* 2018), indicating slower growth. Paradoxically, simultaneous to decreases in size-at-age, age-at-maturity has decreased, when the

opposite would be expected. Decreased age-at-maturity has resulted in age structure truncation through loss of the oldest age classes in many Chinook salmon populations. The most pronounced shifts in age structure have occurred in Alaska, the northern-most part of the species' range (Ohlberger *et al.* 2018). In these populations, the proportion of ocean-age 4 (1.4, or total age 6) has declined from being the prevailing age class in spawning areas, and ocean-age 2 and 3 fish (1.2 and 1.3, age 4 and 5) have more recently become the dominant age classes. Additionally, the oldest, largest fish, ocean-age 5 and older (1.5 or age 7 and up), have become exceedingly rare and have disappeared altogether from many spawning areas (Lewis *et al.* 2015). This change in age structure is particularly concerning because the abundance of Chinook salmon is also declining throughout its range and the ecological consequences of this age structure truncation could inhibit the recovery of this culturally iconic species.

Though the causes of these changes in size and age of Chinook salmon remain unclear, the basin-wide extent of the phenomenon suggests exposure to shared marine drivers may be responsible. A hypothesis to explain the disappearance of older age classes in conjunction with fish returning at smaller sizes and reduced abundances is that ocean mortality is common and selective after the critical periods of ocean entry and the first ocean winter (Beamish and Mahnken 2001; Beamish *et al.* 2001; Schindler *et al.* 2013; Ruggerone 2016). Over time, common late stage marine mortality could preferentially select for early maturity in Chinook salmon, while the fish are still small, through the reduced probability of older fish returning to spawn. Since age at maturity is heritable in this species (Hankin *et al.* 1993; Morita *et al.* 2005; Carlson and Seamons 2008), this selective pressure could result in a genetic change in the maturation reaction norm of these populations (Siegel *et al.* 2018).

Some potential and non-mutually exclusive causes of marine mortality include: changing environmental conditions that affect prey fields, bycatch in marine fisheries, size selective harvest, and changes in the predatory gauntlet of the marine environment. Large-scale climatic phenomena that drive environmental conditions in the North Pacific Ocean, specifically the Pacific Decadal Oscillation (PDO),

have previously been linked to salmon survival and productivity (Mantua *et al.* 1997; Hare *et al.* 1999; Ohlberger *et al.* 2016). However, recent work suggests that the PDO has not been well correlated with salmon abundance in recent decades (Litzow *et al.* 2014; Litzow *et al.* 2016). Ianelli and Stram (2014) estimated the reduction in maturing adults from western Alaskan Chinook salmon populations due to bycatch in the North Pacific Ocean walleye pollock (*Gadus chalcogrammus*) fishery and showed that those reductions were relatively small compared to the scale of the salmon populations. While current evidence suggests size selective harvest has almost certainly played a role in the size changes (Bromaghin *et al.* 2008), Ohlberger *et al.* (2018) reported that exploitation rates in coastal fisheries have declined as demographic changes have accelerated, indicating that size selective harvest alone cannot explain the observed changes. Additionally, Kendall and Quinn (2011) concluded that opposing selection by different fishing sectors suggested other factors contributed to observed size and age trends. Many of these factors cannot be ruled out as contributing to the observed changes in Chinook salmon demographics, yet none alone seems to sufficiently explain the changes that have taken place. Shifts in the predator field faced by Chinook salmon in the ocean is the least examined cause of selective mortality, though evidence of top down effects by predators on Chinook salmon has been increasing. Marine mammals have been shown to consume a significant amount of Chinook salmon, and recent experimental tagging of Chinook salmon at sea suggests that salmon sharks (*Lamna ditropis*) could also be an important predator in some areas (Williams *et al.* 2004; Adams *et al.* 2016; Seitz *et al.* 2016; Chasco *et al.* 2017). However, there has not been a rigorous examination of the potential effects of top down forcing on late marine stage Chinook salmon in the ocean with regards to age structure or body size.

Here we investigated the potential contribution of predators to a "dangerous ocean hypothesis" by performing simulations with a modified version of a published Yukon River Chinook salmon life cycle model (Cunningham *et al.* 2018). The existing model estimated Chinook salmon survival while accounting for environmental covariates and bycatch, but assumed there was no selective late marine

stage mortality after the first ocean winter. Importantly, the existing model did not fully explain the inter-annual variability in spawning ground age structure based on environmentally-driven natural mortality, age-selective marine bycatch mortality, and the estimated change in average marine survival rates across ages. Specifically, the Cunningham *et al.* (2018) estimation model systematically underestimated both the proportion of adults returning after two years in the ocean and the rate at which that proportion is increasing over time. We used this model as a framework to simulate the Chinook salmon life cycle, but added late marine stage mortality to elucidate both the magnitude and selectivity of mortality necessary better to reproduce the observed age structure of an indicator Chinook salmon population in the Yukon River watershed than was possible with environmentally-driven variation in survival and bycatch mortality alone.

Methods

We investigated the impact of late stage mortality on the spawning population dynamics Chinook salmon from the Salcha River, a tributary to the Yukon River, under alternative scenarios describing the intensity and selectivity of additional mortality. The Salcha River represents an optimal indicator for the Yukon River Watershed as it is the largest single producer of Chinook salmon in the drainage (~9% of the spawning population, Brown *et al.* 2017). Additionally, this population has a breadth of data available, such as age, sex, length, and counts of returning adults, and has been used in previous evaluations of Yukon River Chinook salmon production dynamics, including the life cycle model we build on here (Neuswanger *et al.* 2015; Ohlberger *et al.* 2016; Cunningham *et al.* 2018). We utilized the estimated maturation schedule, base-line survival rates at age, capacities, and age-specific fecundities estimated by the stage-structure population dynamics model fit to this population by Cunningham *et al.* (2018) as the basis for our simulations.

To understand tributary-specific changes in the age structure for the indicator population, we examined the observed age structure of adult returns to the Salcha River from 2006 to 2016 as reported by

the Joint Technical Committee (JTC) of the U.S./Canada Yukon River Panel (2007; 2008; 2009; 2010; 2011; 2012; 2013; 2014; 2015; 2016; 2017).We fit a multinomial log linear regression of the ocean age composition of adults returning to the Salcha River by return year (Hosmer Jr. *et al.* 2013) to smooth and identify general trends in the highly variable age structure over time. In multinomial regression, the response variable is y_i with k response categories, $i = 1{:}\,k$, and is the log-odds ratio of a response in category $i = 2{:}\,k$, relative to category 1. Here, y_i is the log-odds ratio of adult returns in an older age class in a given calendar year compared to adults returning after one year at sea, thus our model contains five response categories for ocean ages one through five (k = 5), which represent the majority of the Salcha River spawning population. The age structure was predicted by the single continuous predictor year x, where η is the intercept in response category i, and β is the coefficient on x in response category i. The linear model is:

(2-1) $$y_i = \eta_i + \beta_i x,$$

$$y_i \sim Multinomial(n;\ p_i), i = 1,2,\dots,5;$$

where n is the number of adults returning in a given year and p_i is the probability of those returns belonging to a given ocean age class one through five. Derived from the definition of log-odds, the probability of a fish returning at a specific age and year ($p_i(x)$) is given by:

(2-2) $$p_1(x) = \frac{1}{1+\sum_{i=2}^{k}\exp[\eta_i+\beta_i x]},$$ for ocean-age 1 (the reference age class) and

(2-3) $$p_i(x) = \frac{\exp[\eta_i+\beta_i x]}{1+\sum_{i=2}^{k}\exp[\eta_i+\beta_i x]},\ i = 2,3,4,5,$$ for remaining marine stages.

The predicted proportion of returns of each ocean age class in 2010 was then used as an end point for simulation using the life cycle model. This end point was chosen because the life cycle model was fit using spawning abundance data from 1987 – 2010, as a result 2010 is the final year in which the model can simulate a full age structure. The objective of the simulation exercise was to evaluate the mortality

conditions (i.e., selectivity and intensity) under which the age structure of the observed end point could be replicated.

Stage-structured model modifications

The simulation framework was built from the Bayesian stage-structured estimation life cycle model created by Cunningham *et al.* (2018) that tracks cohorts of Chinook salmon from specific brood years through sequential life stages culminating in spawners returning to the Salcha River (Figure 2-1). By sampling parameter values for the simulation from the joint posterior distribution of the fitted model, we directly incorporated both estimation uncertainty and model structural uncertainty in our predictions. In brief, survival ($SR_{y,s}$) to the next life stage (s) in a given brood year (y) was approximated by a Beverton-Holt transition function (Moussalli & Hilborn, 1986), which is a function of two parameters: productivity, p, and capacity, k:

$$SR_{y,s} = \frac{p_{y,s}}{1+{p_{y,s}N_{y,s-1}}/{k_s}}, \quad (2\text{-}4)$$

where N is abundance from that brood year (y) during the previous life stage (s-1). Productivity is the maximum survival rate to the next life stage and was itself a function of a time-varying basal productivity (Equation 3, Cunningham *et al.* (2018)) and environmental covariates. Environmental covariates were included or excluded at each stage using Bayesian selection methods. Capacity is the total rearing potential of that stage; one capacity parameter was estimated for all freshwater stages and another for all marine stages. Capacity was assumed to not vary with brood year. Basal productivity, or survival before the additive effects of environmental covariates, was found to increase across ocean stages (Cunningham *et al.* 2018). The environmental covariates most strongly supported by the data for the Salcha River population were: (1) ice-out date on the Yukon River, (2) winter temperature in the Pribilof Islands, and (3) Japanese hatchery chum abundance. For additional details on the estimation model used as the basis for simulations see Cunningham *et al.* (2018).

To simulate additional marine mortality, we input additional instantaneous mortality (λ_s) beginning during the first ocean winter to the state equations described by Cunningham *et al.* (2018):

$$N_{y,s} = \left(N_{y,s-1}\right)e^{-\left(S_a \bullet F_t + \lambda_s + M_{y,s}\right)}\left(1 - \phi_a\right). \quad (2\text{-}5)$$

Chinook salmon abundance is represented by $N_{y,s}$ or the number of individuals from brood year y, surviving to the end of stage s. The additional mortality rate of fish in stage s is λ_s, S_a is bycatch selectivity by ocean age a and F_t is the annual bycatch fishing mortality rate in year t, and ϕ_a is the ocean-age specific probability of maturing. Calendar year, t, is offset from brood year, y, based on the timing of each marine stage. Parameter references a, ocean age, and t, calendar year, allow bycatch and harvest to be allocated to the correct spawning year during simulation.

We also accounted for additional mortality when calculating how many individuals would survive to return to the river (equation 9 in Cunningham *et al.* (2018)):

$$R_{t,a} = \left(N_{y,s-1}\right)e^{-\left(S_a \bullet F_t + \lambda_s + M_{y,s}\right)}\left(\phi_a\right)\left(1 - U_{t,p}\right). \quad (2\text{-}6)$$

The number of individuals returning to spawn, $R_{t,a}$, of ocean age a in calendar year t, is the number of surviving individuals, less those caught in terminal commercial, recreational, and subsistence fisheries where $U_{t,p}$ is the year-specific harvest rate.

The number of fish removed by additional mortality from each ocean age class and year were calculated using a modified Baranov catch equation, with our additional mortality substituted for catch:

$$P_{t,s} = \left(\frac{\lambda_s}{S_a \bullet F_t + \lambda_s + M_{y,s}}\right) \cdot \left(N_{y,s-1}\right) \cdot \left(1 - e^{-\left(S_a \bullet F_t + \lambda_s + M_{y,s}\right)}\right). \quad (2\text{-}7)$$

Mortality removals by year and stage are given by $P_{t,s}$. The first term on the right side of Equation 2-7 is the proportion of total mortality (denominator) due to that added in the simulation (numerator), the second term is number of fish entering that stage, and the final term determines the overall mortality rate.

Various values of λ_s, describing the age-specific instantaneous impact rate of additional mortality, were proposed and used to simulate Chinook salmon abundance in calendar years 1987 through 2010. For each additional mortality (λ_s) scenario, uncertainty was simulated by drawing model parameter values from the joint posterior distribution from the Cunningham *et al.* (2018) model. In each year of the simulation, spawner abundance as well as the proportion of females on the spawning grounds in the previous year was identified to calculate population fecundity. Fish advanced from their current stage to the next via the survival rate described by Equation 2-4. The stage and year specific parameters that make up this equation were drawn from their posterior distributions estimated by Cunningham *et al.* (2018). For each ocean stage in a given calendar year, the number of fish removed from the population due to the additional mortality, returning to the river, escaping terminal freshwater harvest, and predicted to arrive on the spawning grounds was recorded. We calculated age structure of returns as the returns from one age class in a given calendar year divided by the sum of all returns that year. The simulation was repeated 100 times for each value of λ_s and the medians of all simulation runs were calculated.

Mortality Scenarios

Mortality scenarios (λ_s) describe additional instantaneous mortality imposed on Chinook salmon of each ocean age (ocean-age 1 through 5). How the additional mortality was apportioned to each age class was given by the selectivity suite (q_s), which was multiplied by a scalar to investigate various levels of total intensity (I). Each selectivity suite summed to one so the value of a given age can be viewed as the proportion of additional mortality (I) allocated to that age class.

(2-8) $\lambda_s = I \bullet q_s$, where s = 1,…,5.

For tracking purposes, scenarios were identified by their selectivity suite number, a dash, and the overall intensity. For example scenario 1-0.5 was selectivity suite 1 multiplied by an instantaneous mortality rate of $I = 0.5$, which equates to an additional 39.3% mortality rate in absence of other sources of mortality. Since the additional mortality resulted in varying numbers of fish removed from the population depending on the number of fish in each ocean age class, we tracked the additional fish removed in a calendar year and calculated percentage of fish removed and total additional realized mortality rate post hoc.

Scenarios consisting of varying intensity and proportion allocated to age classes were explored in a three-phase fashion, where results from one phase informed the design of selectivity suites in the subsequent phase. All selectivity suites were simulated by total intensities of $I = 0 - 2$, in increments of 0.2, meaning that the minimum additional instantaneous mortality rate in a given age class is 0 and the maximum is 2. All suites, prior to scaling by total intensity, are compared in Table 2-1.

When translating the additional instantaneous rates, we must consider that additional mortality takes place simultaneously with fishing mortality and natural mortality predicted by environmental covariates. Therefore to understand the effect of the additional mortality (*AM*) in all scenarios we calculated the ratio of additional mortality to total marine mortality at a given age and year (Equation 2-9). The median additional mortality rate was taken over the simulation period to facilitate the comparison of scenarios. The minimum non-zero and maximum additional mortality rate for each ocean age and selectivity suite are found in the right panel of Table 2-1.

$$AM_{y,s}\,(\%) = \frac{\lambda_s}{\lambda_s + S_a \bullet F_t + M_{y,s}} \cdot \left(1 - e^{-(\lambda_s + S_a \bullet F_t + M_{y,s})}\right) \quad (2\text{-}9)$$

The first phase of simulations consisted of selectivity suites 1 – 4, which when multiplied by the range of intensities resulted in 44 scenarios (e.g., 1-0, 1-0.2, …, 4-2.0). These scenarios were exploratory in nature and were designed to test how additional mortality acted in the model. The next phase of

scenarios consisted of selectivity suites 5 – 9 (55 scenarios) and concentrated additional mortality more heavily around the fourth year at sea, as the proportion of ocean-age 4 and older returns have all but disappeared (Lewis *et al.* 2015; Ohlberger *et al.* 2018). Based on the results of the first two phases of simulations, we tuned selectivity suites 10 – 13 (44 individual scenarios) in phase three to selectively remove ocean-age 3 fish, by forcing all or nearly all of the additional mortality to occur during the third year at sea. Though ocean-age 1s and 5s were included in the analysis, their proportions were relatively low and thus were not critically considered when designing scenarios.

The combination of selectivity suites and intensities from all four phases resulted in a total of 143 scenarios of late marine stage Chinook salmon each of which were independently simulated. Trends in the age structure of simulated adult returns were smoothed using multinomial regression following our previous approach with the spawning ground age composition data. The smoothed age composition in 2010 was compared between the simulation and the observed age structure that year (JTC 2011). We examined a single year for two reasons. First, the time period of the simulations and observations only partially overlap and differ in length. Second, the scenarios are density independent, so the same mortality rates occurred independent of population changes in abundance. As a result of this configuration, the change in the age structure over the simulation period is the same in all scenarios. These two factors make comparing the complete time series nonsensical, while comparing a single year more appropriate. We calculated the log-likelihood of the simulated trend in 2010 given the observed age composition in that year to assess their similarity. The likelihood is given by:

$$(2\text{-}10) \quad L(n, p_i \mid z_i) = \binom{n}{z_i} \prod_{i=2}^{4} p_i^{z_i},$$

where n is the sample size used to generate the observed age structure from 2010 (n = 419), p is the probability of an adult return belonging to ocean age class i in 2010 predicted from observations, and z is the count of adults expected to return in ocean age class i in 2010 from the simulation. The second, third,

and fourth year at sea were included in the log-likelihood calculation while the first and fifth year were not. The contribution of spawning adults from the youngest and oldest age classes were excluded from the log-likelihood calculation because these age classes are rarely observed in the river, thus their proportions are always close to zero and dominated the likelihood calculation when tested. Additionally, because the intensity of late stage mortality is highly uncertain we calculated the total log-likelihood of each selectivity suite integrated over all levels of intensity by summing the log-likelihood of each scenario in a given selectivity suite. By doing so we were able to assess which selectivity suite was most likely to represent the observed trend in age composition, assuming nothing about the total intensity. Finally, we calculated the likelihood ratio of all scenarios compared to the scenario with the highest likelihood and considered the top group of scenarios to be those that are at least half as likely as the top scenario. The simulated total number of returning adults under the leading scenario was plotted against the original estimation model from Cunningham *et al.* (2018), which did not incorporate late stage marine mortality, to qualitatively compare the effect of the scenario on overall population abundance.

Results

The observed proportions of ocean-age 1 and 2 Chinook salmon from the Salcha River increased over time, while the ocean-age 3, 4, and 5 fish decreased over time (Figure 2-2). Specifically, when examining the age structure trends after smoothing via multinomial regression, the proportion of ocean-age 2 fish increased by 11% while the proportion of ocean-age 3 fish showed a decrease of 12% over the time period from 2006 to 2016. The age structure of Chinook salmon returning to the Salcha River predicted from the smoothed trends for 2010 was: 0.28% ocean-age 1, 17% ocean-age 2, 35% ocean-age 3, 45 % ocean-age 4, and 1.1% ocean-age 5.

All scenarios resulted in an additional realized marine mortality of between 0 and 76% during individual ocean years. The post-hoc median realized mortality rate by ocean age and scenario is included as supplemental material (Table S2-1). To produce the observed increase in proportion of ocean-age 2

returns while not driving the proportion of ocean-age 4 returns to extremely low levels, additional mortality had to be concentrated on ocean-age 3 fish. There were 34 scenarios at least half as likely as the top scenario (log-likelihood > -17.74, Table S2-1). These top scenarios were from selectivity suites 8 – 13 which all selectively removed ocean-age 3 fish (Figure 2-3). The realized mortality rates by ocean age class, log-likelihood, and likelihood ratios for all scenarios are included as supplementary material, Table S2-1. The scenario that produced the final age structure which most closely matched the age structure for the smoothed 2010 age proportions from the Salcha River (Figure 2-4) was 10-0.8 (log-likelihood = -9.562, Table S2-1), which removed only ocean-age 3 fish at an intensity of $I = 0.8$. This scenario translates to a median additional mortality rate of 47% on fish entering their third year at sea. The expected age composition of Chinook salmon returning to the Salcha River under scenario 10-0.8 was: 3.3% ocean-age 1, 18% ocean-age 2, 39% ocean-age 3, 36% ocean-age 4, and 3.7% ocean-age 5. Suite eight had the greatest cumulative log-likelihood, which distributed the additional mortality over four ocean age class and had additional mortality rates of 2 – 21%, 4 – 34%, 1 – 10% and 9 – 61% for the second through fifth years at sea, respectively (Figure 2-3). Scenario 10-0.8 resulted in a predicted decrease in adult returns below the lower bound of the 95% Bayesian credible interval from the estimation model fit by Cunningham *et al.* (2018) (Figure 2-5).

Discussion

Through a highly selective scenario, we were able to capture observed changes in the age structure of the Salcha River Chinook salmon population, a representative index stock that like many other populations is showing trends towards smaller and younger fish on the spawning grounds. In this scenario an additional 47% of fish died during their third year at sea surplus to the natural and fishing mortality already implemented in the estimation model. Moreover, all top scenarios contained this highly selective mortality during the third year at sea to reproduce the observed age structure in adult returns. These simulations show that late stage mortality may underpin changes in the spawning age composition of Chinook salmon populations. Given the imperiled nature of many of these populations a critical

reexamination of possible drivers of mortality after the first year at sea is needed to gain a better understanding of demographic dynamics.

The top scenarios suggest that the reduction in abundance of the oldest fish on the spawning grounds is not due to mortality during those latest ocean years, but to lack of survival to these ages. We speculate that mortality of ocean-age 3 Chinook salmon drives age structure on spawning grounds because at this stage, individuals become larger than the average individuals of other salmon species (60 cm fork length and greater) (Groot and Margolis 1991) and thus may become more conspicuous to visual predators. Prior to their third year at sea, other highly abundant salmon species such as pink salmon (*O. gorbuscha*), chum salmon (*O. keta*), or sockeye salmon (*O. nerka*) (Ruggerone and Irvine 2018) may serve as a predation buffer to growing Chinook salmon, reducing the individual risk of being consumed by a predator. Actual observations of predation on ocean-age 3 Chinook salmon corroborate that mortality of this life stage may be selective and intense. Ford and Ellis (2006) compared the species and ages of salmon available to and consumed by resident fish-eating killer whales (*Orcinus orca*) in British Columbia and showed the whales consume ocean-age 3 Chinook salmon at a greater proportion than is present in the environment. Furthermore, Seitz *et al.* (2016) reported 17 of 35 satellite tags deployed on late ocean-age 2 and early ocean-age 3 Chinook salmon outside of Dutch Harbor, Alaska were consumed by predators. Fourteen tags were inferred to be consumed by salmon sharks, two by marine mammals, and one by an ectothermic fish, totaling a 48% mortality rate within 262 days of tagging due to predation. The 48% mortality rate observed in the tagging study is remarkably close to the 47% additional mortality necessary to change the spawning age structure predicted by our simulations. Though the observations of killer whales were highly localized and the tagging study was not designed to compare predation rates between ocean age classes, these occurrences are independent observations of potentially selective and intense predation on ocean-age 3 fish. These observations suggest that some predators frequently consume prey of certain sizes and species, and therefore could act as ecological agents of selection

(MacColl 2011). The corroboration of our simulation exercise and multiple *in situ* predation observations suggests that Chinook salmon could be facing relatively intense and/or selective mortality in the ocean that could contribute to the change in observed age structure.

Though the top scenario concentrated mortality on ocean-age 3 in suite 10, late marine mortality in other age classes is important as well, as demonstrated by the greatest total log-likelihood of suite 8. Suite 8 still reduced survival of fish during their third year at sea but suggested substantial mortality may occur during the second and fifth years as well. This result shows that when no assumptions were made about the intensity, mortality at both ocean-age 2 and 3 are influential. Although suite 8 also contains mortality at ocean-age 5, it is important to remember we did not include the proportion of ocean-age 5 spawners in the log-likelihood calculation. Few fish return to spawn after five years at sea, so changing the contribution of this age group has minimal effect on the overall age structure. Thus, the additional mortality suggested for the oldest fish should be viewed as an artifact of the simulation exercise. The take away from suite 8 is that over a wide range of total intensities selective mortality during both the second and third years at sea appear to be important.

Despite iterative scenario testing, we were not able to create a scenario that captured the observed age structure shift yet did not result in an unrealistic decrease in abundance of returning adults. This could be due to an aspect of Chinook salmon population biology that was not included in the model: the heritability of age at maturity and how that age can respond to selective pressure (Hankin *et al.* 1993; Morita *et al.* 2005; Carlson and Seamons 2008). Given a smaller proportion of older-maturing individual returnuing to spawn, the lifetime reproductive success of individuals exhibiting this phenotype would be reduced. Over time this could result in a genetic change in the maturation schedule of these populations. For convenience and interpretability, the maturation schedule in the estimation model upon which our simulation framework is based was held constant across time. Earlier maturation would require the removal of fewer individuals to observe the same shift in age structure. The combination of earlier

maturation and common, selective mortality could create that age structure shift without such large reductions in overall returns. Recent work on western Alaskan Chinook salmon using growth histories derived from scale analysis provides evidence that the age threshold for maturation has indeed declined in recent decades (Siegel *et al.* 2018). Additionally, simulation work including the heritability of maturation showed that Chinook salmon that experience selective exploitation can experience reductions in the size and age of maturation on the scale of decades (Bromaghin *et al.* 2008). Given the observed decline in maturation threshold, the history of exploitation of this species, our results, and the limitations of the model structure we used, we believe that selective and/or intense mortality through predation can play a part in shaping age structure through sheer removal of individuals. However, observed changes are more likely due to the removal of individuals at ocean-age 3 in conjunction with longer-term evolutionary changes in the timing of maturation.

We do not propose that all observed changes in Chinook salmon demographics are attributable to one agent of selection such as predation. Many of the challenges facing Chinook salmon populations apply selective pressure in the same direction and could exert a cumulative evolutionary effect. Other factors include: selective harvest, bycatch at sea, the influence of climactic factors, and competitive effects with hatchery salmon. Chinook salmon have long been subject to harvest and although harvest rates have been variable through this species' range and have declined in some areas, harvest is still a mortality source during the late marine stage. Though the impact of bycatch at sea on its own is estimated to be minimal and not very selective (Ianelli and Stram 2014; Cunningham *et al.* 2018), bycatch is another source of marine mortality for Chinook salmon after their first year at sea. Additionally, favorable ocean conditions since the 1977 regime shift and hatchery propagation of Pacific salmon has led to more salmon in the ocean, resulting in apparent density-dependent effects (Ruggerone and Irvine 2018). An increasingly crowded ocean could lead to individual fish risking more predation exposure to procure prey and thus experiencing increased marine mortality (Godin 1997; Ahrens *et al.* 2012), coupled with reduced

growth opportunity. These factors highlight the alignment of several selective pressures in the ocean, which may be individually insignificant, but could compound to exert directional selection for younger age of maturation in Chinook salmon.

The shift in age structure to younger returning adults likely has a further indirect effect by reducing the intrinsic reproductive potential of Chinook salmon populations. This reduction may result from smaller fish having smaller eggs, reduced fecundity, slower swimming speeds, and reduced ability to dig redds, among other fitness consequences (Healey 1991; Allendorf *et al.* 2008). Further compounding these potential ecological effects is the possibility of increasing the skewed sex ratio of adult returns in this species. Chinook salmon are known to have distorted and sometimes extreme sex ratio bias with more male returns than females (Halupka *et al.* 2000; Olsen *et al.* 2006), despite even sex ratios of individuals going to sea. Presumably due to increased fitness benefits of size-dependent fecundity, female Chinook salmon mature at a larger size and older ages than males (Healey 1991) and therefore are exposed to more mortality risk in the marine environment. Some rivers and tributaries have experienced dramatic shifts to low proportions of female returns, which may be reducing the effective population productivity for a given spawning abundance. These rivers include: the mainstem Yukon (33% female) and Gisasa rivers (29.6% female), a tributary to the Yukon River (JTC 2017); the Tuluksak River (31% female), a tributary to the Kuskokwim River (Webber and Harper 2018); and the Killey River (28% female), a tributary to the Kenai River (Gates and Boersma 2016). Selective late stage marine mortality could lead to even lower proportions of female returns, which would lead to decreased population fecundity and further reduced population productivity.

Highly selective mortality at sea in addition to environmentally driven variation in survival provides a previously unexamined mechanism to account for demographic changes. The nature of the selectivity and intensity found to best approximate observed changes in age structure are generally consistent with marine predators. Our simulations demonstrate that marine mortality after that first year

may influence the age structure. Given this result, the remaining years at sea should not be dismissed as inconsequential. Taken as a whole, our results call for a critical reexamination of a longstanding hypothesis in salmon biology that the ocean is a generally safe place for salmon after their first year at sea, during which the year class strength is set (Beamish and Mahnken 2001). We suggest that while year class *strength* may indeed be determined during the first year at sea, population *age structure* may be determined by selective agents later in the marine stage. Perhaps not surprising, these effects appear the most pronounced in our study species, Chinook salmon, that rear in the ocean longer than other Pacific salmon. In light of the continued depression on Chinook salmon stocks, a critical re-examination of late stage mortality is needed given its apparent role in determine age structure, which in turn can indirectly act as an additional bottleneck to productivity.

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Tables and Figures

Table 2-1: Selectivity suites (q_s) determines how additional predation is applied to each ocean age class. (Left Panel) Selectivity suites as instantaneous mortality rates in log space prior to scaling by predation intensities (I) of from 0 – 2.0 to form predation scenarios (λ_s). These scenarios were applied to stock of Chinook salmon from the Salcha River, which served as an indicator stock for other Chinook salmon populations. (Right Panel) Range of annual mortality rates produced by all predation scenarios when environmentally driven and bycatch mortality are accounted for.

		Instantaneous Mortality Rate (q)					**Additional Mortality Rate (AM, %)**				
		Ocean Ages					**Ocean Ages**				
		1	**2**	**3**	**4**	**5**	**1**	**2**	**3**	**4**	**5**
Selectivity Suite	**1**	0.20	0.20	0.20	0.20	0.20	0.03 – 0.21	0.03 – 0.25	0.03 0.28	0.03 – 0.29	0.04 – 0.31
	2	0.00	0.05	0.05	0.45	0.45	0.00	0.01 – 0.07	0.01 – 0.07	0.08 – 0.54	0.08 – 0.56
	3	0.07	0.13	0.20	0.27	0.33	0.01 – 0.08	0.02 – 0.18	0.03 – 0.28	0.05 – 0.37	0.06 – 0.45
	4	0.33	0.27	0.20	0.13	0.07	0.04 – 0.33	0.04 – 0.32	0.03 – 0.28	0.02 – 0.21	0.01 – 0.12
	5	0.04	0.04	0.43	0.43	0.04	0.01 – 0.05	0.01 – 0.06	0.07– 0.49	0.07 – 0.52	0.01 – 0.08
	6	0.03	0.10	0.17	0.34	0.34	0.01 – 0.04	0.02 – 0.14	0.03 – 0.24	0.06 – 0.45	0.06 – 0.46
	7	0.00	0.08	0.42	0.42	0.08	0.00	0.01 – 0.12	0.07 – 0.48	0.07 – 0.51	0.02 – 0.14
	8	0.00	0.16	0.26	0.05	0.53	0.00	0.02 – 0.21	0.04 – 0.34	0.01 – 0.09	0.09 – 0.61
	9	0.00	0.00	0.91	0.09	0.00	0.00	0.00	0.14 – 0.73	0.02 – 0.15	0.00
	10	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.15 – 0.75	0.00	0.00
	11	0.00	0.00	0.90	0.10	0.00	0.00	0.00	0.14 – 0.73	0.02 – 0.16	0.00
	12	0.00	0.00	0.80	0.20	0.00	0.00	0.00	0.12 – 0.69	0.03 – 0.29	0.00
	13	0.00	0.00	0.70	0.30	0.00	0.00	0.00	0.11 – 0.65	0.05 – 0.40	0.00

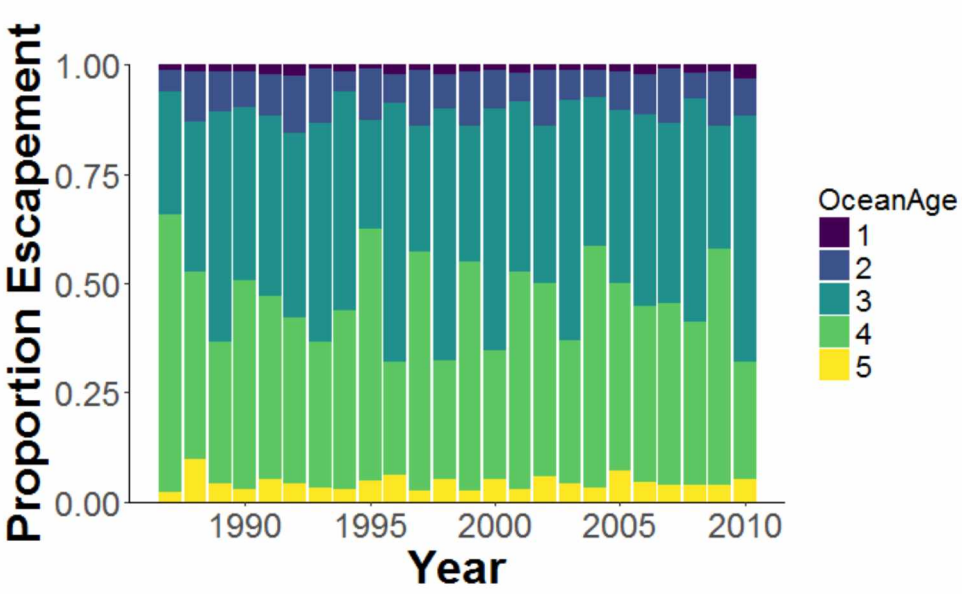

Figure 2-1: The age structure of adult Chinook salmon returning to the Salcha River estimated by the Cunningham *et al.* (2018) prior to the addition of the predation scenarios. The time series of age composition is the starting point for all simulations carried out in this study.

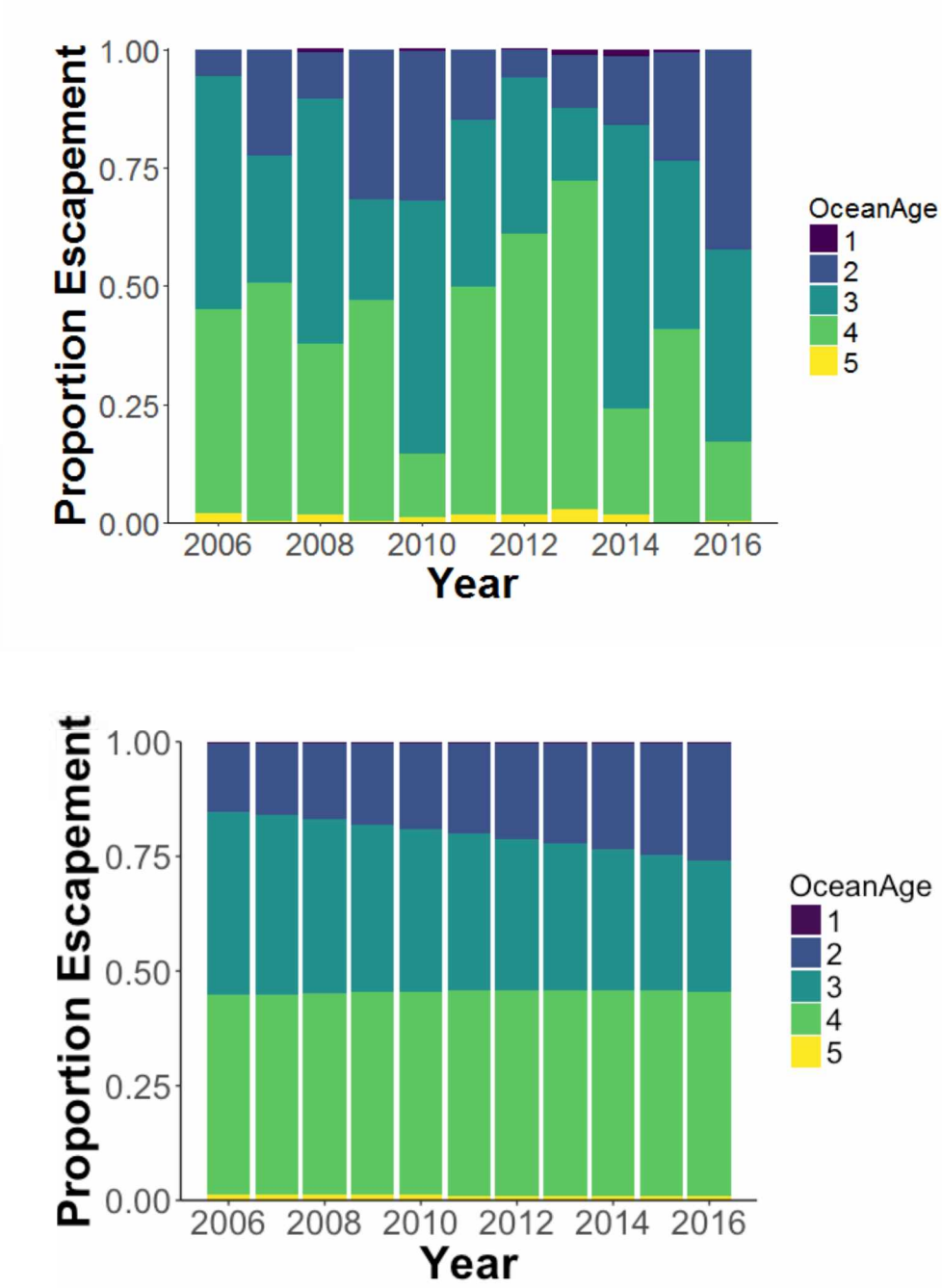

Figure 2-2: (Top Panel) Observed proportions of Chinook salmon adult returns to the Salcha River from 2006 – 2016 (JTC 2007; 2008; 2009; 2010; 2011; 2012; 2013; 2014; 2015; 2016; 2017). (Bottom Panel) Trend in proportion of Chinook salmon adult returns to the Salcha River based on the multinomial regression of observed returns from 2006 – 2016.

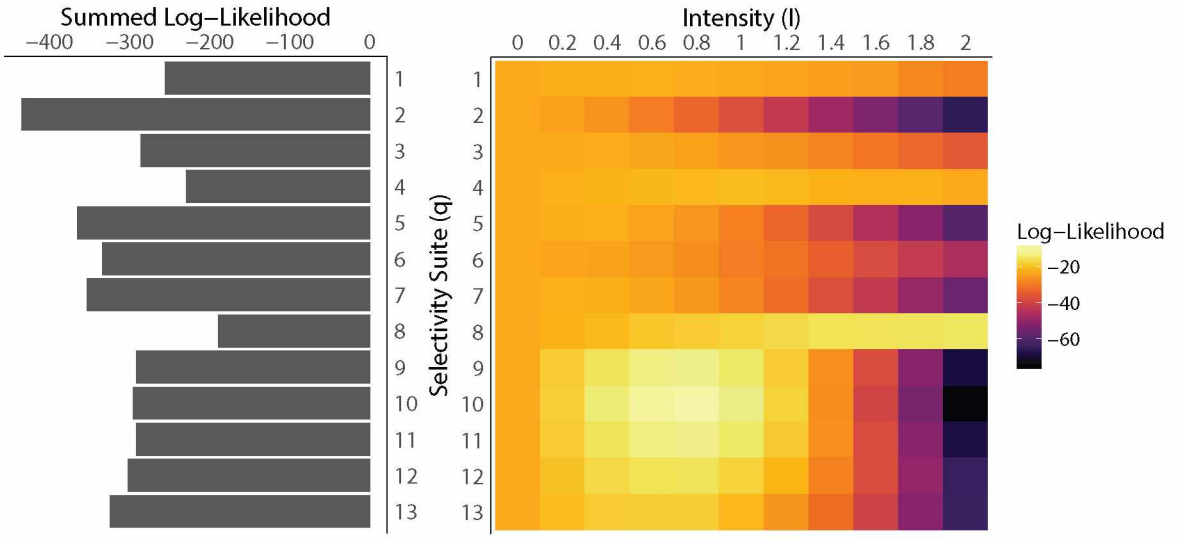

Figure 2-3: (Right Panel) Heat map of the log-likelihoods of all scenarios by selectivity suite (q) and overall intensity (I). (Left Panel) Total likelihood for each selectivity suite integrated over all intensities.

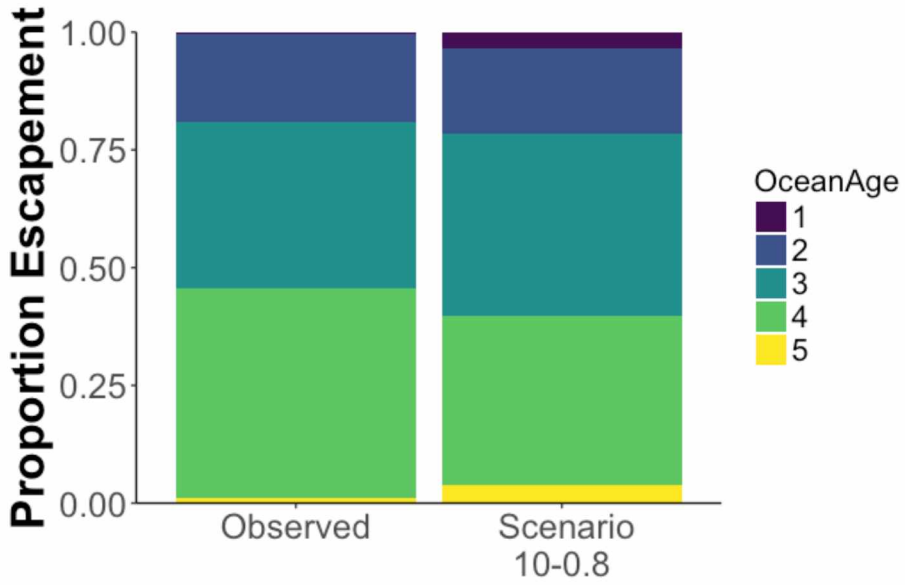

Figure 2-4: Comparison of the predicted age structure of adult Chinook Salmon returns to the Salcha River in 2010 (left) and scenario 10-0.8 in 2010, which applied additional mortality to ocean-age 3 at a rate of 47% (right).

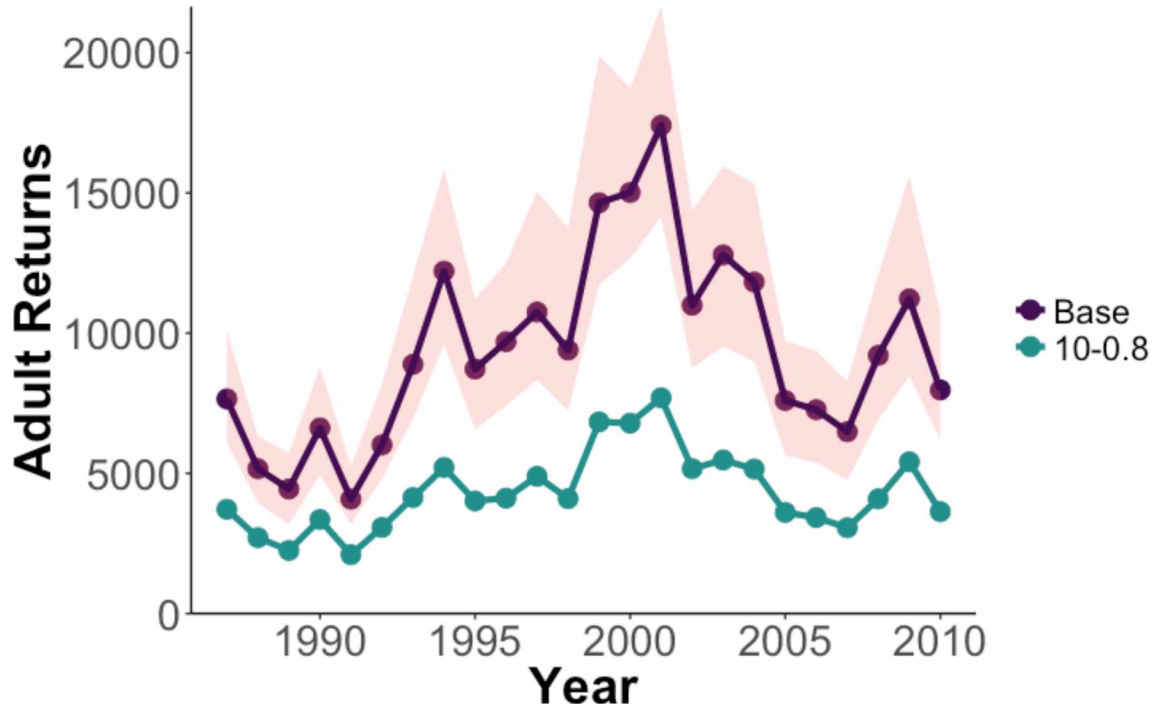

Figure 2-5: Simulated abundance of adult returns under the scenario 10-0.8 plotted against the original model fit. Note how the scenario causes the adult return to fall outside of the 95% Bayesian credible interval of the original model fit.

Supplementary

Table S2-1: The median additional mortality rate (%), log-likelihood and likelihood ratio for all 143 scenarios, ordered by log-likelihood of the predicted simulation output given the predicted observed age composition.

ID	1	2	3	4	5	Log-likelihood	Likelihood Ratio
10-0.8	0.00	0.00	0.47	0.00	0.00	-9.56	1.00
10-0.6	0.00	0.00	0.38	0.00	0.00	-10.38	1.09
9-0.8	0.00	0.00	0.44	0.06	0.00	-11.49	1.20
11-0.8	0.00	0.00	0.43	0.07	0.00	-11.68	1.22
10-1.0	0.00	0.00	0.54	0.00	0.00	-11.84	1.24
9-0.6	0.00	0.00	0.35	0.05	0.00	-12.02	1.26
11-0.6	0.00	0.00	0.35	0.05	0.00	-12.23	1.28
10-0.4	0.00	0.00	0.28	0.00	0.00	-12.87	1.35
11-1.0	0.00	0.00	0.50	0.08	0.00	-13.46	1.41
9-1.0	0.00	0.00	0.51	0.08	0.00	-13.46	1.41
8-2.0	0.00	0.21	0.34	0.09	0.61	-13.93	1.46
11-0.4	0.00	0.00	0.25	0.03	0.00	-14.33	1.50
9-0.4	0.00	0.00	0.25	0.03	0.00	-14.33	1.50
12-0.8	0.00	0.00	0.40	0.13	0.00	-14.40	1.51
8-1.8	0.00	0.19	0.32	0.08	0.57	-14.42	1.51
12-0.6	0.00	0.00	0.32	0.10	0.00	-14.57	1.52
8-1.6	0.00	0.17	0.29	0.07	0.53	-14.62	1.53
8-1.4	0.00	0.15	0.26	0.06	0.49	-14.75	1.54
8-1.2	0.00	0.13	0.23	0.05	0.44	-15.67	1.64
12-0.4	0.00	0.00	0.23	0.07	0.00	-15.95	1.67
12-1.0	0.00	0.00	0.47	0.16	0.00	-16.67	1.74
10-1.2	0.00	0.00	0.60	0.00	0.00	-16.81	1.76
8-1.0	0.00	0.11	0.19	0.05	0.38	-16.89	1.77
10-0.2	0.00	0.00	0.15	0.00	0.00	-17.09	1.79
13-0.6	0.00	0.00	0.29	0.15	0.00	-17.28	1.81
13-0.8	0.00	0.00	0.36	0.19	0.00	-17.56	1.84
13-0.4	0.00	0.00	0.20	0.10	0.00	-17.60	1.84
8-0.8	0.00	0.09	0.16	0.04	0.32	-17.60	1.84
11-0.2	0.00	0.00	0.14	0.02	0.00	-17.69	1.85
9-0.2	0.00	0.00	0.14	0.02	0.00	-17.69	1.85
9-1.2	0.00	0.00	0.57	0.09	0.00	-17.74	1.85
11-1.2	0.00	0.00	0.56	0.10	0.00	-17.86	1.87
8-0.6	0.00	0.07	0.12	0.03	0.25	-18.38	1.92
12-0.2	0.00	0.00	0.12	0.03	0.00	-18.75	1.96

4-1.0	0.19	0.18	0.15	0.11	0.06	-19.32	2.02
13-0.2	0.00	0.00	0.11	0.05	0.00	-19.43	2.03
8-0.4	0.00	0.05	0.08	0.02	0.18	-19.81	2.07
4-1.2	0.22	0.21	0.18	0.13	0.07	-19.94	2.09
4-0.6	0.12	0.11	0.09	0.07	0.04	-20.15	2.11
4-0.8	0.15	0.14	0.12	0.09	0.05	-20.20	2.11
13-1	0.00	0.00	0.42	0.23	0.00	-20.25	2.12
12-1.2	0.00	0.00	0.52	0.19	0.00	-20.28	2.12
4-0.4	0.08	0.08	0.06	0.05	0.02	-20.58	2.15
4-1.4	0.25	0.24	0.20	0.15	0.08	-20.83	2.18
8-0.2	0.00	0.02	0.04	0.01	0.09	-20.90	2.19
1-0.6	0.07	0.08	0.09	0.10	0.10	-21.14	2.21
5-0.4	0.01	0.01	0.13	0.14	0.02	-21.22	2.22
4-0.2	0.04	0.04	0.03	0.02	0.01	-21.26	2.22
7-0.2	0.00	0.01	0.07	0.07	0.02	-21.38	2.24
4-1.8	0.30	0.29	0.25	0.19	0.10	-21.39	2.24
4-1.6	0.28	0.27	0.23	0.17	0.09	-21.42	2.24
7-0.4	0.00	0.02	0.13	0.14	0.03	-21.49	2.25
1-0.4	0.05	0.06	0.06	0.07	0.07	-21.58	2.26
1-0.2	0.03	0.03	0.03	0.03	0.04	-21.58	2.26
5-0.2	0.01	0.01	0.07	0.07	0.01	-21.67	2.27
1-0.8	0.10	0.11	0.12	0.13	0.14	-21.80	2.28
3-0.4	0.02	0.04	0.06	0.09	0.12	-21.81	2.28
3-0.2	0.01	0.02	0.03	0.05	0.06	-21.92	2.29
1-1.0	0.12	0.14	0.15	0.16	0.17	-22.05	2.31
1-0.0	0.00	0.00	0.00	0.00	0.00	-22.09	2.31
10-0.0	0.00	0.00	0.00	0.00	0.00	-22.09	2.31
11-0.0	0.00	0.00	0.00	0.00	0.00	-22.09	2.31
12-0.0	0.00	0.00	0.00	0.00	0.00	-22.09	2.31
13-0	0.00	0.00	0.00	0.00	0.00	-22.09	2.31
2-0.0	0.00	0.00	0.00	0.00	0.00	-22.09	2.31
3-0.0	0.00	0.00	0.00	0.00	0.00	-22.09	2.31
4-0.0	0.00	0.00	0.00	0.00	0.00	-22.09	2.31
5-0.0	0.00	0.00	0.00	0.00	0.00	-22.09	2.31
6-0.0	0.00	0.00	0.00	0.00	0.00	-22.09	2.31
7-0.0	0.00	0.00	0.00	0.00	0.00	-22.09	2.31
8-0.0	0.00	0.00	0.00	0.00	0.00	-22.09	2.31
9-0.0	0.00	0.00	0.00	0.00	0.00	-22.09	2.31
4-2.0	0.33	0.32	0.28	0.21	0.12	-22.09	2.31
3-0.6	0.03	0.06	0.09	0.13	0.17	-22.27	2.33
7-0.6	0.00	0.04	0.18	0.20	0.04	-22.33	2.34

6-0.2	0.00	0.02	0.03	0.06	0.06	-22.56	2.36
1-1.2	0.14	0.16	0.18	0.19	0.20	-22.66	2.37
5-0.6	0.02	0.02	0.19	0.20	0.02	-22.88	2.39
6-0.4	0.01	0.03	0.06	0.11	0.12	-23.05	2.41
2-0.2	0.00	0.01	0.01	0.08	0.08	-23.30	2.44
3-0.8	0.03	0.08	0.12	0.17	0.22	-23.32	2.44
1-1.4	0.16	0.18	0.20	0.22	0.23	-23.66	2.47
6-0.6	0.01	0.05	0.08	0.17	0.17	-24.18	2.53
1-1.6	0.18	0.21	0.23	0.24	0.25	-24.32	2.54
7-0.8	0.00	0.05	0.24	0.25	0.06	-24.54	2.57
5-0.8	0.02	0.03	0.24	0.26	0.03	-24.69	2.58
3-1.0	0.04	0.09	0.15	0.21	0.26	-24.70	2.58
13-1.2	0.00	0.00	0.48	0.27	0.00	-24.97	2.61
2-0.4	0.00	0.01	0.01	0.15	0.15	-25.45	2.66
3-1.2	0.05	0.11	0.18	0.24	0.31	-25.60	2.68
9-1.4	0.00	0.00	0.62	0.11	0.00	-25.74	2.69
11-1.4	0.00	0.00	0.61	0.12	0.00	-25.82	2.70
6-0.8	0.02	0.06	0.11	0.21	0.22	-25.95	2.71
10-1.4	0.00	0.00	0.65	0.00	0.00	-25.96	2.72
1-1.8	0.20	0.23	0.25	0.27	0.28	-26.49	2.77
6-1.0	0.00	0.06	0.28	0.30	0.07	-27.23	2.85
3-1.4	0.06	0.13	0.20	0.28	0.35	-27.53	2.88
12-1.4	0.00	0.00	0.58	0.22	0.00	-27.80	2.91
5-1.0	0.03	0.03	0.29	0.31	0.04	-27.83	2.91
1-2.0	0.22	0.25	0.28	0.29	0.31	-28.43	2.97
2-0.6	0.00	0.02	0.02	0.21	0.22	-28.69	3.00
6-1.0	0.02	0.07	0.13	0.26	0.27	-28.71	3.00
3-1.6	0.07	0.14	0.23	0.31	0.38	-29.93	3.13
6-1.2	0.03	0.09	0.16	0.30	0.31	-30.29	3.17
13-1.4	0.00	0.00	0.53	0.30	0.00	-30.90	3.23
7-1.2	0.00	0.07	0.33	0.35	0.09	-30.99	3.24
3-1.8	0.07	0.16	0.25	0.34	0.42	-32.01	3.35
2-0.8	0.00	0.03	0.03	0.27	0.28	-32.21	3.37
5-1.2	0.03	0.04	0.34	0.36	0.05	-32.26	3.37
6-1.4	0.03	0.10	0.18	0.34	0.36	-33.48	3.50
3-2.0	0.08	0.18	0.28	0.37	0.45	-34.79	3.64
2-1.0	0.00	0.03	0.04	0.32	0.34	-36.50	3.82
7-1.4	0.00	0.08	0.37	0.39	0.10	-36.52	3.82
12-1.6	0.00	0.00	0.62	0.24	0.00	-37.11	3.88
9-1.6	0.00	0.00	0.66	0.12	0.00	-37.13	3.88
11-1.6	0.00	0.00	0.66	0.13	0.00	-37.17	3.89

6-1.6	0.03	0.11	0.20	0.38	0.39	-37.29	3.90
5-1.4	0.04	0.04	0.38	0.41	0.05	-37.71	3.94
10-1.6	0.00	0.00	0.69	0.00	0.00	-39.04	4.08
13-1.6	0.00	0.00	0.58	0.34	0.00	-39.49	4.13
6-1.8	0.04	0.13	0.22	0.41	0.43	-41.24	4.31
2-1.2	0.00	0.04	0.04	0.37	0.39	-41.58	4.35
7-1.6	0.00	0.09	0.41	0.43	0.12	-41.65	4.36
5-1.6	0.04	0.05	0.42	0.45	0.06	-44.17	4.62
6-2.0	0.04	0.14	0.24	0.45	0.46	-45.26	4.73
2-1.4	0.00	0.05	0.05	0.42	0.44	-46.98	4.91
7-1.8	0.00	0.10	0.45	0.47	0.13	-48.66	5.09
12-1.8	0.00	0.00	0.66	0.27	0.00	-49.66	5.19
11-1.8	0.00	0.00	0.70	0.15	0.00	-50.95	5.33
5-1.8	0.05	0.06	0.46	0.49	0.07	-51.05	5.34
9-1.8	0.00	0.00	0.70	0.13	0.00	-51.16	5.35
13-1.8	0.00	0.00	0.61	0.37	0.00	-51.17	5.35
2-1.6	0.00	0.05	0.06	0.46	0.48	-52.65	5.51
10-1.8	0.00	0.00	0.73	0.00	0.00	-54.02	5.65
7-2.0	0.00	0.12	0.48	0.51	0.14	-55.87	5.84
2-1.8	0.00	0.06	0.06	0.50	0.52	-58.99	6.17
5-2.0	0.05	0.06	0.49	0.52	0.08	-59.50	6.22
13-2	0.00	0.00	0.65	0.40	0.00	-63.89	6.68
12-2.0	0.00	0.00	0.69	0.29	0.00	-64.41	6.74
2-2.0	0.00	0.07	0.07	0.54	0.56	-65.74	6.87
11-2.0	0.00	0.00	0.73	0.16	0.00	-68.47	7.16
9-2.0	0.00	0.00	0.73	0.15	0.00	-68.86	7.20
10-2.0	0.00	0.00	0.76	0.00	0.00	-75.93	7.94

General Conclusion

This thesis was a first step in investigating the potential role of predation, with an emphasis on salmon sharks as predators of Chinook salmon throughout their marine range. In Chapter 1, I gathered all available information on salmon shark energetics and diets, and used three methods to gain an understanding of the energetic requirements of this shark species. The results suggested that salmon sharks could consume as much prey as a similar-sized marine mammal, but the estimates were highly uncertain. Additionally, because of several knowledge gaps about salmon sharks, it was not possible to estimate this species' impacts on Chinook salmon, or any prey species, with confidence. In Chapter 2, I used a new tool to examine the effects of additional mortality on a Chinook salmon population while accounting for bottom-up environmental effects, harvest, and bycatch. Through an exploration of theoretical scenarios, I showed that mortality during the third year in the ocean could produce the observed shifts in Chinook salmon age structure observed in an indicator stock in Alaska.

An exciting result of this study was that heavy mortality on ocean-age 3 Chinook salmon predicted by this modeling exercise aligned with observations of wild predation events. Ford and Ellis (2006) compared the species and ages of salmon available to and consumed by resident killer whales (*Orcinus orca*) in British Columbia and showed the whales preferentially consume ocean-age 3 Chinook salmon. Seitz and Courtney (2016) also reported 17 of 35 satellite tags deployed on late ocean-age 2 and early ocean-age 3 Chinook salmon outside of Dutch Harbor, Alaska were consumed by predators including salmon sharks (*Lamna ditropis*), marine mammals, and an ectothermic fish. The vast majority of tags that showed signs of predation, 14 of 17, were inferred to have been eaten by salmon sharks, based on their unique visceral temperature. The alignment of an independent simulation exercise with recorded mortality events suggests that predation could be a top-down driver of adult Chinook salmon age structure.

The value of this research lies in the new identification of a life history stage of Chinook salmon when population-level impacts on age structure may be occurring. Salmon sharks also appear to consume Chinook salmon at a stage sensitive in the determination of population age structure. By examining both predatory biology and prey population dynamics perspectives, I was able to draw initial conclusions about the potential importance of this predator-prey relationship. Namely, salmon sharks show energetic requirements similar to those of a like-sized marine mammal and those requirements could translate to the consumption of a substantial biomass of prey. Taken together these conclusions point to a potential mechanism of top-down predation pressure during a critical period for Chinook salmon populations.

The obvious major limitation of this research is that currently there are not sufficient data to corroborate these results. Thus, I could draw preliminary conclusions from the results, but could not test their plausibility. This lack of validation was most apparent in the estimate of salmon shark prey requirements examined in Chapter 1. Many direct estimates of energetic requirements depend on understanding metabolic rates, which can be determined from respirometry, the measurement of oxygen consumed by an organism. Respirometry studies have not been performed on any adult lamnid including salmon sharks, though juvenile lamnids and smaller shark species have been examined (Graham *et al.* 1990; Sepulveda *et al.* 2007). The logistics of placing a large free-swimming animal into a highly specialized piece of equipment which is not available at all marine labs are not trivial, yet not insurmountable.

In Chapter 2, the comparisons of simulation results to observations of predations also have limitations. . For example, it is unclear how generalizable the killer whale observations are throughout their range and caution is warranted applying observations in one part of the range to others. Additionally, salmon shark predation events were inferred from Seitz *et al.* (2016); however, this study was not designed to compare marine mortality among age classes. So, though frequent predation was observed on ocean-age 3 fish, it is unknown if this predation rate is higher than other age classes. To compare

predation rates in-situ, equal numbers of Chinook salmon of different ages would need to be tagged and the results compared. However, such a study poses serious logistical challenges as capturing and tagging older, less-common age classes would be difficult and the current large size of satellite tags precludes their use with younger, smaller age classes.

I did not generate a population level consumption estimate as doing so would require salmon shark diet composition and total population abundance. Conducting a diet study with a large number of individuals and an estimate of population abundance both pose significant challenges. Diet studies are often lethal, which may not be ethical in a long-lived species with relatively low reproductive output. Non-lethal methods, such as gastric lavage, are impractical when working with a large sharp-toothed, often ill-tempered, focal species. Future investigators may be confined to using salmon shark stomachs from bycatch fatalities, which would not give the diet study geographic coverage over the range of the species and could bias diet results to the species targeted in commercial fisheries. Estimating population abundance for fishes is often done through mark-recapture or catch per unit effort studies, both of which would be challenging to execute for a fast-swimming, broadly distributed species like the salmon shark. These challenges will have to be overcome to robustly quantify the impact of salmon shark predation on Chinook salmon at a population level.

Though at this time I was not able to determine the actual, realized effects of salmon sharks on Chinook salmon, this study still sheds light on key knowledge gaps about the North Pacific food web and highlights what could be a sensitive time in Chinook salmon life history. This research suggests the reexamination of a longstanding hypothesis in salmon biology, which is that the ocean is a fairly safe place for salmon after their first year at sea, during which the year class strength is set (Beamish and Mahnken 2001). The finding that marine mortality after that first year may influence the age structure indicates that the remaining years at sea should not be dismissed as inconsequential. In light of the continued depression on Chinook salmon stocks, maybe it is time to supplement the critical size, critical

period hypothesis for population regulation with another critical period, specifically conditions in the 3rd ocean year, that determines age structure and can act as an additional bottleneck to productivity.

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